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**The establishment of dominance in
male jewel skinks, *Carlia jarnoldae*:
the roles of displays, body size
and colouration**

Thesis submitted by Sarah Maclagan in partial fulfilment of the requirements for the Degree of Bachelor of Science with Honours in the School of Tropical Biology at James Cook University.



Male *Carlia jarnoldae*

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I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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ABSTRACT

During the establishment of social relationships, many animals use displays to communicate about fighting ability or territory holding capacity. Typically, scincid lizards are cryptically coloured, and thought to have rudimentary social behaviour not involving contests or territoriality. Male jewel skinks (*Carlia jarnoldae*), however, exhibit bright colouration, use relatively complex social displays, and appear to be territorial. I examined the social and physical contexts of displays used during the establishment of dominance between pairs of males in experimental enclosures. I also determined whether body size, the colour (i.e., hue, value, chroma) of three colour patches (green-blue throat, blue dorso-lateral spots and orange flanks), or the size of the orange flank patch were associated with dominance, and tested the prediction of “sequential assessment game” theory that contests should be more escalated when opponents are most similar in body size or colour area. In my experimental enclosures, the lizards almost always (26/33) formed dominant-subordinate relationships within the first 48 hours of contact. Head bobbing and tail waving appear to be important means of opponent assessment in this species, as lizards spent more time engaging in these displays when they first interacted than a day later. Dominants displayed significantly more than subordinates on both observation days. The lizards displayed most in environmental contexts that maximised their conspicuousness, i.e., head bobs and tail waves both occurred more often on a raised platform, in the centre of the enclosure, and in the sun, whereas tail waving, which is the most conspicuous behaviour, also occurred frequently on the flat sandy substrate of the enclosures. Displaying on raised surfaces, in central locations, and in the sun probably enhances the efficiency of communication of specific displays. I found that body size was a very strong predictor of dominance in *C. jarnoldae*, but that the colours of the three patches were not. A trend for dominants to have larger orange patches relative to their body size than did subordinates approached significance, suggesting that colour patch size may also influence the outcome of dominance relationships. Orange patch size may be more important in nature, acting as a long-distance visual cue to territory ownership and fighting ability, allowing individuals to avoid escalated conflicts by assessing each other from afar. Contrary to the predictions of the sequential assessment game, escalation increased rather than decreased with the difference between opponents in body mass, and did not decrease over time, suggesting that dominant male jewel skinks will not tolerate intruders within their territory, and continue to escalate contests even with repeated intrusions by the same individual. In general, male *Carlia jarnoldae* use displays to communicate with conspecifics, and form social relationships that give the dominant individual priority of access to shelter and display sites. Body size is an important

determinant of the outcome of contests, and orange colour patch size may be a cue allowing assessment of body size in this species. Dominant individuals do not tolerate intruders, suggesting that these species are territorial in nature. Thus, *Carlia jarnoldae* do not fit the typical pattern for skinks, but are more similar to other taxa of lizards that are highly social and territorial.

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GLOSSARY

Chroma: saturation, of or pertaining to a colour.

Diurnal: primarily active during the day.

Fossorial: associated with the ground or subsurface.

Hue: colour as determined by position of wavelengths within the visual spectrum (i.e., “green” or “blue”).

SVL: snout-to-vent length

Value: greyness, of or pertaining to a colour.

Behaviours of *Carlia jarnoldae*:

Head Bob: rapid up and down movement of the head.

Tail Wave: side-to-side movement of the entire tail.

Distal Third: subdued tail wave in which only the distal third portion of the tail is waved.

Gape: wide opening of the mouth.

Throat Flash: sideways tilt of the head at a 90° angle.

Head Tilt: sideways tilt of the head at a less-than-90° angle.

Bask Flat: dorsoventral flattening of the body against the substrate.

Bask Normal: head raised but forebody resting on substrate.

Bask High: head and forebody raised off substrate by full extension of the forelimbs.

Body Lift: head and entire body raised off substrate by full extension of the forelimbs and hindlimbs.

Lateral Tilt: posture such that body is tilted to one side.

HEDGING ONE'S PARENTAL BETS

(Completed during initial project, "Intra-clutch variation in egg provisioning by frogs of the Australian Tropical Savanna")

ABSTRACT

Plants and animals have a great diversity of parental investment strategies to maximize their fitness. They vary in the number of clutches produced within breeding seasons and over entire life spans; the number and size of offspring among clutches; and even in the degree of variability in investment in each offspring within a single clutch. Restrictions on the values of these traits are imposed by tradeoffs between current and future reproduction and between the size and number of offspring produced at once, and also by the degree of temporal environmental variability to which organisms are exposed. In a constant environment, organisms should evolve a canalized, optimal form of any trait. In a predictably variable environment, organisms may evolve phenotypic plasticity. However, when environments vary unpredictably, organisms should evolve bet-hedging tactics, which maximize geometric mean fitness across generations. Bet-hedging can involve spreading reproductive investment across time and varying the amount invested in offspring among or within clutches. In this paper I review parental investment strategies involving diversified bet-hedging in temporally unpredictable environments, and provide an overview of the evidence so far.

INTRODUCTION

Any organism's primary goal is to reproduce (Roff 1992). The rate of reproduction is strongly affected by how organisms allocate their reproductive effort among offspring and over time. Plants and animals have evolved an enormous diversity of parental investment strategies to maximise their rates of reproduction.

Parental investment strategies vary greatly in the distribution of reproductive effort over time. Iteroparous species produce a number of batches of offspring throughout their lifetime, while semelparous species concentrate all their reproductive effort into one "big bang", and then die (Roff 1992). Within iteroparous species, parents may produce batches continuously, once or many times during an annual breeding season, or only every few years. Within semelparous species, parents may produce propagules with variable diapause duration (Hopper 1999), or dormancy times (Capinera 1979), as an alternative way to spread offspring production through time.

Tremendous variation also exists in the strategies parents use to partition their reproductive effort between offspring size and number. The general trend is that organisms either produce few relatively large offspring, or many relatively small ones. For example, a blue whale produces a single large calf at once, while a sturgeon releases tens to hundreds of millions of tiny eggs in a single spawning event (Stearns 1993). Differences also occur in the degree of *variation* in size of propagules, not only among related species (e.g. nematodes: Poulin & Hamilton 2000; salamanders: Wilbur 1977), but also among individuals within populations (e.g. bees: Kim & Thorp 2001; frogs: Luddecke 2002), between the successive clutches of a single individual (e.g. snails: Baur & Baur 1997; lizards: Olsson & Madsen 2001; terrapins: Roosenburg & Dunham 1997), and even within a single clutch. Considerable within-clutch variation in offspring size occurs in various species of plants (Harper *et. al* 1970, Capinera 1979), birds (Lack 1947, O'Connor 1978, Herbert & Sealy 1993, Forbes 1999), reptiles (Hays *et. al* 1993), fishes (Mazzoldi *et. al* 2002), insects (Capinera 1979), and amphibians (Crump 1981, Crump 1984; Kaplan & King 1997; Lips 2001).

The diversity of possible reproductive investment strategies is affected by both evolutionary tradeoffs (which will be discussed later in more detail), and by the degree of environmental uncertainty to which organisms are exposed. Environmental uncertainty in climate, resource availability, predation pressure, and competition can influence how females partition resources among offspring and clutches (Lips 2001). If environmental conditions are constant, organisms should evolve a canalized, “optimal” egg or clutch size (Capinera 1979). When conditions vary predictably, organisms may evolve phenotypic plasticity, which results in environmentally cued, non-random responses (Lips 2001). However, when conditions vary unpredictably, recent theory suggests organisms should evolve a “bet-hedging” strategy, in which investment is partitioned such that at least some offspring will survive, no matter what environmental conditions are encountered (Seeger and Brockmann 1987). Parents may achieve this by dispersing their offspring through time (by being iteroparous, or by producing offspring with variable dormancy times), or across an environment-specific fitness gradient (by producing offspring with variable phenotypes), or both.

In this paper I will review the role of bet-hedging in parental investment strategies evolved within temporally varying environments. I will first provide a background on the theory of bet-hedging, then discuss how parental investment strategies are shaped by various tradeoffs. Finally, I will discuss the available evidence for parental bet-hedging. Although “parental investment” can potentially encompass a broad range of reproductive activities such as courtship, territorial defence, and parental care, my use of the term is restricted to its simplest meaning, propagule production. Furthermore, my review will only consider bet-hedging in plants, and in animals that do not provide parental care.

BET-HEDGING

The term “bet-hedging” was first used in the context of reproductive strategies by Slatkin (1974) in a response to Gillespie’s observation (1974) that selection can favour repeated production of smaller clutches of offspring (iteroparity) over the production of a single large clutch (semelparity), because it reduces variance in parental fitness. The term has since been expanded to include any trait that reduces variance in fitness over generations, even if it entails a ‘sacrifice’ of expected fitness within any given generation (Philippi & Seger 1989).

The concept of bet-hedging at first appears paradoxical – it suggests that there are exceptions to the rule that natural selection favours traits that maximize an individual’s expected number of surviving offspring. The theory of bet-hedging claims that if an environment varies temporally, phenotypes with low variances of fitness may be favoured over alternatives with higher variances, even if the alternatives have higher mean fitnesses.

The apparent paradox is resolved by closer examination of the way in which “fitness” is calculated. Because evolution occurs over time, what matters is the increase or decrease in gene frequencies over generations of reproduction (Hopper 1999). Therefore, when the fitness of a genotype varies over generations, the appropriate measure of its relative growth rate is the geometric mean of fitness across generations, not the arithmetic mean of the fitness distribution (Gillespie 1974). Equal to the n th root of the product of n numbers, the use of the geometric mean allows for the fact that fitness is determined by an inherently multiplicative process, and not an additive one (Seger & Brockmann 1987, Simons 2002).

In an unchanging environment, the number of individuals surviving in each generation will be equal, and the geometric and arithmetic means will be the same. However, if the numbers vary even slightly, the geometric mean will always be less than the arithmetic mean; and the more variable the numbers, the smaller the geometric mean becomes (Seger & Brockmann 1987; Yoshimura & Jansen 1996). Consequently, the geometric mean fitness of a genotype can be increased by reducing the variance of its fitness (over generations), even if the reduction of variance also entails a reduction in the arithmetic mean (Philippi & Seger 1989). In contrast, the arithmetic mean will overestimate fitness to an increasing degree with increasing variance among generations. For example, if the fitness of a genotype in any one year is zero, the geometric mean drops automatically to zero, as the genotype has gone extinct (Yoshimura and Jansen 1996). The arithmetic mean, however, will remain an average of genotypic fitnesses in surrounding years.

To summarise, the appropriate measure for genotypic fitness across generations is the geometric mean, and this can be maximized by reducing the variance in fitness between generations,

even if it entails a reduction of the arithmetic mean. Seger and Brockmann (1987:182) thus described bet-hedging as “a tradeoff between the mean and variance of fitness”.

Simons (2002) pointed out that this description is based on a misconception; because the correct measure of fitness across generations is the geometric mean, and this is maximized by decreasing intergenerational variance, there is no tradeoff. He asserted that the geometric mean is *always* the appropriate intergenerational measure of fitness, and so “the assumption that expected or within-generation fitness is maximized by natural selection is simply wrong” (Simons 2002: 692). He attributed the persistence of “the misguided tradeoff idea” to the fact that it reconciles the more accessible view of selection - that organisms are selected towards an optimal state for a given environment - with the more accurate view - that organisms are selected towards an optimal state given a series of different environments (Simons 2002: 692). Although Simons is correct that selection should always maximise geometric mean fitness, all previous studies have focused on the concept of tradeoffs, and I will restrict my review to cases of bet-hedging which do sometimes reduce the arithmetic mean in order to maximise geometric mean fitness.

Types of Bet-Hedging

Seeger and Brockmann (1987) placed bet-hedging strategies into two categories: ‘conservative’ and ‘diversified’. The authors liken conservative bet-hedging to the adage “a bird in the hand is worth two in the bush”. As suggested by the saying, conservative bet-hedging occurs when the advantage of experiencing very high success (catching the two birds) even most of the time does not offset the disadvantage of suffering very low success (losing all birds) even occasionally. The geometric mean fitness is instead maximized by avoiding both extremes and adopting a ‘safe’ intermediate (keeping one bird) all the time. Hopper (1999) suggests that in a sense, this conservative strategy might be better named ‘risk-aversion’ than ‘bet-hedging’, since the strategy is to always bet that the environment will be adverse.

Human behaviour often involves conservative bet-hedging, a prime example being the investment in insurance policies (Seeger & Brockmann 1987). Although insurance costs more than it is expected to return in the form of benefits (and so on average it reduces the wealth of its customers), it is deemed beneficial because it reduces *variance* in wealth by preventing total financial disasters (Seeger & Brockmann 1987).

The other form of bet-hedging, ‘diversified’, can be likened to another common saying, “don’t put all your eggs in one basket” (Seeger & Brockmann 1987). In this strategy, reduced variance in the fitness of a genotype *across* generations is achieved by *increasing* variation in fitness among individuals *within* generations (Philippi & Seger 1989). This is achieved by increasing

variation in the phenotypic expression of a single genotype, and hedges against the chance of environmental change by ensuring that whatever environmental conditions eventuate, some offspring will be well-suited (Hopper 1999).

To find an example of diversified bet-hedging in the human world, we need not look past its name. ‘Bet-hedging’ is the practice of gamblers at race tracks who bet money on several horses in the same race to increase their average gains (Stearns 1993).

An example (adapted from Philippi & Seger 1989) will further clarify the distinction between conservative and diversified bet-hedging, and show how both can confer higher geometric mean fitness than specialized genotypes under conditions of unpredictable environmental variability. Suppose a haploid annual plant population occurs in an environment where ‘wet’ and ‘dry’ years occur randomly, but with equal frequency. There are four different genotypes, whose fitnesses can be calculated as follows:

Year Type	Genotype			
	Wet-year Specialist	Dry-year Specialist	Conservative Bet-hedger	Diversified Bet-hedger
Wet	1.0	0.6	0.785	0.8
Dry	0.58	1.0	0.785	0.79
Arithmetic Mean	0.79	0.8	0.785	0.795
Geometric Mean	0.762	0.775	0.785	0.795

(Note that the numbers in this model can vary, as long as the fitness of the conservative bet-hedger is less than the arithmetic mean of the fitness of the two specialists). Within each type of year, the appropriate specialists have the highest fitness. However, these specialists both do poorly in the wrong type of year, and thus their geometric mean across years is low. It is irrelevant that their arithmetic means are high, as selection will act to maximize the geometric mean. The conservative bet-hedger does equally well in both year types, and although its best is far worse than either of the specialists’ bests, its worst is far better. This is reflected by its higher geometric mean fitness. Finally, the diversified bet-hedger does better across generations than any of the other genotypes, because some individuals do well every year and only some do poorly.

Unless the production of variable phenotypes is costly, or it is possible to produce offspring that perform better in at least some environments than the arithmetic mean of the performance of specialist genotypes, a conservative bet-hedger will have lower fitness than a diversifying bet-hedger that produces appropriate phenotypes specialized for each environment in rough proportion to the likelihood of each environment being encountered (Kaplan & Cooper 1984; Hopper 1999). I will concentrate on diversified bet-hedging in the remainder of this review.

Mechanisms of Diversified Bet-Hedging

Little is known about how within-genotype phenotypic variation is produced in diversified bet-hedging (Cooper & Kaplan 1982, Simons & Johnston 1997). Cooper and Kaplan (1982) suggested that random phenotypic variation may be produced by “adaptive coin flipping”, whereby the developmental path is determined by a chance event, like the flip of a coin. Although the authors admitted they did not know what mechanisms are likeliest to be used as ‘coins’, they suggested three broad categories as logical possibilities. These are: (1) unresolved developmental noise - variation which cannot be attributed to either genetic factors or to environmental circumstances, but which is brought about by intangible internal sources of variation; (2) physiological noise - the temporary values of physiological variables; and (3) environmental noise – random and apparently irrelevant signals from the environment (Cooper & Kaplan 1982).

Simons and Johnston (1997) advocated developmental noise as the most likely mechanism, and proposed that this could arise from selection for developmental instability in traits. The authors explained that traits with low developmental stability are more sensitive to the effects of the environment, and may therefore exhibit more developmental noise. They argued that rather than being regarded as a detrimental “inability to stabilize”, developmental instability may be better regarded as “the ability to destabilize development” to increase phenotypic variation in bet-hedging traits (Simons & Johnston 1997: 405).

Whatever the mechanism, it should be noted that the phenotypic diversification produced by diversified bet-hedging differs in a number of ways from a mixed evolutionarily stable strategy (ESS; after Maynard Smith 1982, in Krebs & Davies 1993). A mixed ESS may be produced either by a genetic polymorphism, or by individual genotypes that express both phenotypes (Krebs & Davies 1993). In contrast, a diversified bet-hedging strategy is the variable phenotypic expression of a single genotype (Seger & Brockmann 1987). Although both genetic polymorphisms and diversified bet-hedging are favoured by environmental variability, they often require different conditions for evolution, and their underlying mechanisms are different (Hopper 1999). Genetic polymorphisms do not reduce the variance of an individual genotype’s fitness – they reduce the variance of the population’s mean fitness (Seger & Brockmann 1987). In contrast, diversified bet-hedging reduces the variance of fitness at the level of an individual genotype (Seger & Brockmann 1987). Therefore, genetic diversity would be less reliable as an adaptation to unpredictable but recurrent instabilities, since selection during one season could produce individuals with inappropriate adaptations for the next season (Capinera 1979). If the cost of phenotypic variation within a genotype is not too high, a single genotype with a variable phenotype can invade and

replace a genetic polymorphism that includes the same phenotypes expressed by separate genotypes (Cooper & Kaplan 1982, Hopper 1999).

PARENTAL INVESTMENT STRATEGIES

Producing offspring is expensive. For example, in reptiles, between 5% and 20% of the annual energy budget is usually spent on egg laying (Congdon *et. al* 1982, in Clutton-Brock 1991). In birds, the daily energetic costs of producing eggs are around 29-35% of basal metabolic rate, and daily protein requirements increase by between 86% and 230% (Robbins 1983, in Clutton-Brock 1991). Due to these energy demands, the benefits of current reproduction are usually balanced by a cost, in terms of future growth, survival or fecundity (Wilbur 1977, Roff 1992). 'Costs of reproduction' may include: depletion of an organism's resources, leaving it more prone to sources of mortality such as disease, hypothermia, etc.; greater risk from predators while seeking a mate, either because of increased time spent away from safe havens such as burrows, or because the activities associated with mate attraction (such as calling and displaying) also attract predators; and increased vulnerability of reproductive females to predators due to increased visibility or reduced mobility (Roff 1992).

Because reproduction is costly in terms of energy and there is a finite amount of energy available to parents for investment into offspring, various tradeoffs occur. Tradeoffs are the linkages between two or more traits that constrain their simultaneous evolution (Stearns 1993). The two tradeoffs most relevant to parental investment are between current and future reproduction (i.e., the cost of reproduction), and between quality and number of offspring.

Semelparity vs. Iteroparity

Whether semelparity or iteroparity is the optimal life history strategy depends on the balance between the benefits of current reproduction (in terms of progeny) and its costs (in terms of mortality or future reproduction; Hautek ete *et. al* 2001). A substantial number of studies have shown that production of offspring is associated with reductions in a parent's subsequent survival or breeding success (Clutton-Brock 1991). If the costs are so high that death after first reproduction is certain, a parent will have no reason to conserve resources, and semelparity will be favoured (Gadgil & Bossert 1970, Roff 1992). However, if it is possible for a parent to avert death by investing less than the maximal possible amount into reproduction (and hence conserving some energy for its own survival), it may increase its lifetime reproductive success by surviving to reproduce again (Roff 1992, Kaitala *et. al* 2002).

Because an individual's reproductive potential is highest at its first reproduction, all life-history models agree that semelparous organisms should achieve a higher reproductive output than iteroparous organisms (Stearns 1993, Kaitala *et. al* 2002). In support of this prediction, there is evidence that reproductive effort is greater in many semelparous organisms than in closely related iteroparous organisms (Roff 1992, Stearns 1993, Hautek ete *et. al* 2001).

However, the environment also plays a major role in determining life histories, by shaping variance in juvenile and adult survival (Gadgil & Bossert 1970, Stearns 1993, Benton & Grant 1999). Environments often vary unpredictably over time, and both juveniles and adults may be vulnerable to changes in environmental quality. If adult survival is more variable than juvenile survival, semelparity will be favoured because it is uncertain whether parents will live to breed again (Gadgil & Bossert 1970, Roff 1992). However, if juveniles are more vulnerable to temporarily harsh environments, and environmental quality cannot be predicted by parents, it may be beneficial for parents to produce a number of clutches over a period greater than the time scale of environmental variation (Wilbur 1977, Schultz 1989, Benton & Grant 1999, Hopper 1999). In this way, iteroparity increases the chances that at least some offspring will experience favourable conditions, and so reduces the variance in parental fitness. Thus, iteroparity may be considered a form of bet-hedging, because although it may reduce mean reproductive output, it can increase the geometric mean of parental fitness by reducing within-generation variance in fitness (Stearns 1993). These conclusions are supported by the results of a model by Jonsson and Ebenman (2001), which showed that semelparous organisms face a higher risk of extinction than iteroparous organisms under such circumstances.

Interestingly, Benton and Grant (1999) found that very strong environmental variability selects not only against semelparity, but also against iteroparity over an extremely long reproductive life, since variability selects for an increase in energy diverted to reproduction to minimize the risk of death before significant reproductive success is attained. The authors nevertheless concluded that in a variable environment, semelparity is the ESS in only 3.5% of cases, while iteroparity is the rule (Benton & Grant 1999).

However, other authors have found that semelparity can sometimes evolve in a temporally variable environment by using alternative mechanisms to reduce reproductive uncertainty (Real & Ellner 1992, Benton & Grant 1999). For example, semelparous plants with variation in seed dormancy duration, and insects with variation in diapause duration can achieve functional iteroparity (Wilbur 1977, Hopper 1999). Evidence for bet-hedging via variation in dormancy times of offspring will be considered below.

Offspring Size vs. Number

Whether parents reproduce once or many times, there is always a finite amount of energy available to be channeled into offspring at any one time. In species that produce more than one offspring, this energy must be split between offspring. There are two “intuitively obvious” relationships with regards to patterns of energy expenditure by parents: (1) as the energy expended on individual offspring increases, the number of offspring that parents can produce decreases; and (2) as the energy expended on individual offspring increases, the fitness of individual offspring increases (Smith & Fretwell 1974: 499). These relationships result in a tradeoff between the size and number of offspring an individual can produce. Substantial circumstantial evidence has been found to support this tradeoff, particularly when comparisons are made between closely related species (Clutton-Brock 1991, Roff 1992). For example, in birds (Lack 1947), fish (Wootton 1979), amphibians (Salthe 1969), and reptiles (Derickson 1976, Ferguson & Fox 1984), species that have relatively larger eggs or neonates typically produce small clutches or litters.

Many models have attempted to predict the optimal strategy for dividing parental investment among offspring, based on this tradeoff. The classic model by Smith and Fretwell (1974) has been the basis of most subsequent work. Their model assumed that there is a finite amount of energy available for reproduction at any given time, and that a minimum level of investment is required before an offspring can survive at all (Figure 1a, point M); and above this point, offspring fitness increases at a constantly decreasing rate with increasing parental investment (i.e., is monotonically increasing; Figure 1a).

Optimal egg size under these conditions can be derived graphically by finding the point at which a straight line from the origin is tangent to the offspring fitness curve (Figure 1a, point A). This is the point at which the slope (representing offspring fitness returned per unit parental investment), and thus parental fitness, is maximized (Figure 1b, point A). Other investment strategies will provide lesser returns of parental fitness (e.g., Figure 1a and 1b, points B and C). The Smith-Fretwell model

therefore predicted that there is a single optimal offspring size that maximizes parental fitness. An extended interpretation of this result is that equal investment in all young represents the theoretical optimal strategy.

However, the validity of one of the main assumptions of the Smith-Fretwell model, that offspring fitness is a monotonically increasing function of size, has been questioned. Capinera (1979) disagreed that larger propagule size necessarily confers greater fitness. Instead, he argued that under any particular set of conditions, a certain intermediate size is often optimal. For example, when planted at a depth of 6cm, seedlings from large flax seeds emerge faster than those from small seeds; at a depth of 1cm small seeds emerge more quickly; and at 3cm there is no significant difference in germination time (Harper & Obeid 1967, in Capinera 1979). Hence, large seeds are only at an advantage when buried deeply, perhaps because they have difficulty obtaining sufficient water for germination due to their lower surface area to volume ratio (Harper & Obeid 1967, in Capinera 1979).

Wilbur (1977) argued that there are a number of possible shapes the fitness function may take, depending on the selective mechanism producing it. These include: (1) a power function (such as the one suggested by Smith and Fretwell); (2) a parabolic function in which survival increases to a maximum at some intermediate offspring size then declines at larger sizes (such as the one suggested by Capinera); (3) a concave upward function; and (4) a linear function. He explains that different fitness functions predict different optimal offspring sizes, and that variation in offspring size may result from a number of different fitness functions acting at once. Whatever the shape of the offspring fitness function, it seems likely that parental fitness only increases up to a certain point of offspring size, after which it becomes increasingly beneficial for a parent to produce more offspring.

Another major limitation of the Smith-Fretwell model is that it does not consider environmental variability, and therefore predicts that the optimal parental strategy is to divide reproductive effort evenly between offspring of a single optimal size. Winkler and Wallin (1987) also used this assumption, and predicted that variation in total reproductive effort of individuals within a population should be greater than variability in effort per offspring within individual clutches, because the latter depends on fewer variables. However, different environments are likely to produce different fitness functions, which in turn will favour different offspring sizes. Given this, in spatially or temporally heterogeneous environments it may be advantageous for organisms to produce a *range* of offspring sizes (Capinera 1979; Kaplan & Cooper 1984; McGinley 1987).

McGinley *et. al* (1987) modelled the effect of temporal environmental variation on the optimal parental investment strategy. They compared three parental strategies in an environment

with only two states, good and bad: (1) parents are capable of predicting environmental quality and adjusting offspring size accordingly, (2) parents produce offspring of only one size every year (the size optimal for good years, the size optimal for bad years, or an intermediate), and (3) parents produce a combination of small and large offspring each year. They varied the difference in quality between good and bad years, and the frequency of good years (see Table 1).

TABLE 1: Results of simulations by McGinley *et.al* (1987) calculating the optimal offspring size in a temporally variable environment, using geometric mean as a measure of fitness. S = small offspring only, M = medium-sized offspring only, L = large offspring only, and V = both large and small offspring.

Probability of a Good Year	Difference in Quality Between Years				
	2	3	4	6	8
0.2	M	M	M=L	M=L	M=L
0.5	M	M	V	V	V
0.8	M	V	V	V	V

The authors found that parents adopting strategy 1 (anticipating environmental change and acting accordingly) always have the highest fitness. However, when parents are unable to predict environmental conditions, the optimal strategy varies. When there is not much difference in quality between good and bad years, the production of uniform, intermediate-sized offspring is favoured. When there is a great difference between good and bad years, and a low probability of good conditions, it is optimal to produce uniform, large offspring. However, when there is a great difference between years, but a high probability of a good year, variable offspring production is favoured. By producing variable offspring under these conditions, parents can increase their total number of offspring surviving in good years, while safeguarding against total failure in bad years. This can be seen as a form of bet-hedging, because although parents do not make as many offspring as they could in a good year, they never suffer total disaster because they always have at least some offspring which are well-suited to the prevailing environment.

Parental Investment Strategies in Variable Environments

We have seen that in theory, temporally unpredictable environments can favour parents who hedge their bets by spreading their offspring either through time, or across an environment-specific fitness gradient (in our example, size). Each of these represents a different solution to the same problem of unpredictable fluctuations in environmental quality. In a particularly variable environment, it is possible that some organisms may employ both tactics simultaneously (i.e., produce a number of clutches over time, each containing a range of offspring sizes). However, in many cases it is likely that the geometric mean can be increased sufficiently by one tactic or the

other. Schultz (1989) thus predicted that semelparous organisms should show greater offspring phenotypic variance than iteroparous organisms. Data on variation in seed morphology among annual and longer-lived species of the genus *Crepis* agrees with this prediction (Silverton 1985, in Schultz 1989). Of course, which strategy is used will depend on the relative costs of each in a particular species. For example, if the production of phenotypic variation carries a cost, and parental survival after first reproduction is possible, iteroparity should be selected (Schultz 1989).

EVIDENCE FOR PARENTAL BET-HEDGING

Although theoretical models have demonstrated that temporal environmental heterogeneity can lead to bet-hedging, their significance remains to be demonstrated by convincing empirical studies (Roff 1992, Stearns 1993, Hopper 1999). Hopper (1999) suggests the lack of good evidence may be due to the failure of most models to provide detailed, testable hypotheses. While there is no shortage of studies that claim to demonstrate bet-hedging (usually when phenotypic variation is greater than expected), these have rarely been tested thoroughly enough to exclude other, equally plausible explanations for observed patterns. For example, McGinley (1987) argues that a non-adaptive reason why phenotypic variation should be greater in variable environments is that canalizing selection is weaker.

Hopper (1999) suggested some broad predictions that should be tested before bet-hedging can be invoked. The fitness of bet-hedging parents should be greater than that of non-bet-hedging parents under variable environmental conditions. Furthermore, the phenotypic variation produced by bet-hedgers should increase with increasing environmental uncertainty. Finally, in diversified bet-hedging, variation in phenotypes must result from a single genotype, so studies must eliminate the possibility that observed variation is due to genetic sources (Hopper 1999).

Recent interest in bet-hedging has focused on the germination behaviour of seeds, the diapause behaviour of insects, and parental control of offspring size (Philippi & Seger 1989).

Spreading Offspring Through Time

Many plants and insects use a specialized morphological and physiological state to avoid temporarily harsh conditions, referred to as dormancy (plants) or diapause (insects; Harper *et. al* 1970, Bull 1987, Hopper 1999). This enables members of a population to remain insulated from recurrent or sporadic environmental hazards, and so ensures the continuation of the population through unfavourable seasons or environmental catastrophes (Harper *et. al* 1970). In many plants and insects, variation has been observed in the dormancy times of individuals produced by a single

parent within a single reproductive event. This has been interpreted as bet-hedging in response to the unpredictable duration of unfavourable conditions.

Plants. The first ever application of diversified bet-hedging was Cohen's model for the germination of desert annual plants (Philippi & Seger 1989). Seeds that germinate risk suffering a bad year (e.g. frost or drought), but seeds that do not germinate risk mortality while dormant. Thus a seed that remains dormant has a smaller expected contribution to future generations than does a seed that germinates, but there may be many years in which germination will prove universally lethal (Cohen 1966, in Philippi & Seger 1989). Cohen's model made several testable predictions: (1) seeds that do not germinate under good conditions in the first year should germinate under those same conditions in subsequent years; (2) within a species, the fraction of seeds that germinate each year should correlate with the average amount and predictability of rainfall; and (3) each parental genotype should produce seeds that germinate in different years (Cohen 1966, in Philippi & Seger 1989).

Philippi (1993) found support for all three predictions in a desert annual species, *Lepidium lasiocarpum*, from Arizona. Seeds were germinated in an environmental chamber set up to simulate the natural temperatures and photoperiod of the region. Each year, seeds were watered until no more seeds germinated in that year. Sixty-four percent of the seeds germinated in the first year, and 44% of the remainder germinated in the second year (supporting prediction 1). Seeds were also collected from field sites with different average amounts of rainfall, and the fraction of seeds germinating in the first year was perfectly rank-correlated with mean rainfall (prediction 2). Finally, seeds collected from individual plants germinated in both the first and second years (prediction 3).

There is also support for bet-hedging in a few other desert plants (Venable 1989, Claus & Venable 2000; in Menu & Desouhant 2002). However, there is little evidence for bet-hedging in plants from more temperate areas (Menu & Desouhant 2002).

Insects. For insects with several generations per year, there is often a time in the year when it is beneficial for individuals to enter diapause rather than developing directly (Philippi & Seger 1989). If unfavourable conditions always arrive on the same date, a population should switch abruptly from direct development to diapause. However, when the date of onset is unpredictable, a diversified bet-hedging strategy may be favoured in which a fraction of individuals undergo direct development while others enter diapause (Philippi & Seger 1989).

Although this pattern has been observed a number of species including *Wyeomyia smithii* (pitcher-plant mosquitoes), *Oncopeltus fasciatus* (milkweed bugs), *Corythucha spp.* (lace bugs) and *Trypoxylon politum* (mud-dauber wasps; Philippi & Seger 1989), Hopper (1999) concluded in his review that there is still very little clear evidence that satisfies the predictions of theory. According

to theory, in environments with unpredictable lengths of favourable seasons, the proportion of individuals entering diapause should increase during the favourable season as the likelihood of completing another generation declines (Hopper 1999). Thus, a gradual increase in the proportion of individuals diapausing as the season progresses would indicate bet-hedging, as long as the variation in diapause frequency is not genetically determined (Hopper 1999).

Studies on *Caledia captiva* in south-eastern Australia (Groeters 1994) and *Deois flavopicta* in central Brazil (Fontes *et. al* 1995) both observed that females laid batches including diapausing and directly-developing eggs, with the proportion diapausing increasing as the season progressed. Both authors suggested that bet-hedging may account for the observed variation in diapause behaviour, but neither measured the fitness costs of diapausing or developing directly, nor did they examine the possibility that variation was genetically based.

A series of experiments, models, and observations on *Allonemobius socius* (Bradford 1991, Bradford & Roff 1993, 1995, 1997; all in Hopper 1999) thoroughly investigated all the predictions of bet-hedging theory, but found that very little bet-hedging occurs in this species. Although females lay mixtures of diapausing and non-diapausing eggs with the proportion diapausing increasing as the season progresses, this gradual increase results from variation among females, while in contrast, the switch is very rapid within females. Furthermore, variation among females had a strong genetic component.

Given the lack of clear evidence, Hopper (1999) concluded that genetic differences and phenotypic responses to environmental cues explain most of the phenotypic variation in insect diapause, while year-to-year variation in favourable season length is often too small to select for bet-hedging. However, Menu and Desouhant (2002) argue that Hopper's review did not consider species with prolonged diapause, which they believe are good models with which to test bet-hedging theory. Prolonged diapause occurs when a proportion of larvae diapause for one or more years, hedging against the chance that entire years may occasionally be unsuitable for reproduction (Philippi & Seger 1989, Menu *et. al* 2000, Menu & Desouhant 2002). Indeed, these species often live in environments with a high level of unpredictable variation, a situation in which bet-hedging is expected to evolve (Menu & Desouhant 2002).

Menu *et. al* (2000) modeled various diapause strategies in the chestnut weevil, *Curculio elepha*. They found that in small, isolated populations, a diversified bet-hedging strategy (with emergence after one or two years) was fitter than a simple diapause strategy (emergence after one year) or fixed prolonged diapause strategy (emergence after two years). In a follow-up study, Menu and Desouhant (2002) found that larval weight and emergence date depend on pre-diapause environmental conditions such as temperature and food. These factors cannot be used to predict the

quality of the next year, which depends on factors such as soil drought, predation and fungal attack. Thus, the authors concluded that the chestnut weevil uses plastic responses to unpredictable environmental variation to create phenotypic variation for diversified bet-hedging (Menu & Desouhant 2002). Philippi and Seger (1989) suggested that diapause behaviour in insects with prolonged diapause should receive more research attention.

Spreading Reproductive Energy into Phenotypically Variable Offspring

As stated in the introduction, relatively high intraclutch variation in propagule size occurs in many species, from a diverse range of taxa. Most papers attribute this intraclutch variation (ICV) to bet-hedging in unpredictable environments (e.g. Capinera 1979, Crump 1981, Lips 2001). However, in order to show that bet-hedging really is the cause, these observations need to be supported by data showing that offspring of different sizes have differential success and that the degree of ICV is correlated with environmental unpredictability. The possibility of genetic causes for variation must be eliminated. Although many studies have investigated the effects of offspring size on fitness, and a few have shown that ICV increases with environmental unpredictability, there is, to my knowledge, no study that has tested both predictions simultaneously. Thus, to date, there is no clear and undisputable evidence that ICV is used as a bet-hedging strategy by plants or animals.

The best evidence so far comes from amphibians. Many amphibian species show marked intra-clutch variation, and they tend to breed in temporary freshwater habitats, which typically show strong temporal variation in habitat quality (Griffiths 1997, Williams 1997, Alford 1999). For example, at the beginning of the wet season when pools first fill, there is ample food and there are few predators or competitors to contend with. However, as the wet season progresses, habitat quality deteriorates as food becomes a limiting resource, predators and competitors increase in density, and the risk of desiccation increases (Griffiths 1997). Thus, amphibians are ideal candidates for the study of intraclutch variation as a bet-hedging strategy.

Many studies have examined the effect of initial egg size on larval fitness in amphibians. A number of authors have found that egg size has a positive effect on initial size of hatchlings (e.g. Crump 1984, Williamson & Bull 1989, Kaplan 1992, Tejedo & Reques 1992), however, under ideal conditions, these size differences usually do not persist until metamorphosis (e.g. Crump 1984, Andr n *et. al* 1989, Williamson & Bull 1989, Parichy & Kaplan 1992, Tejedo & Reques 1992). In contrast, under conditions of competition, larger tadpoles have often outcompete smaller tadpoles (reviewed in Alford 1999). The greater success of larger larvae may be due to their ability to competitively exclude smaller larvae from food sources (e.g. Savage 1952, Steinwascher 1978). Furthermore, larger tadpoles may be better able to avoid predators. For example, Parichy and Kaplan

(1995) found that *Bombina orientalis* tadpoles from larger eggs had faster sprint swimming speeds. The results of the above studies generally agree that greater egg size increases the fitness of tadpoles, however, it is important to realize that the strength of this relationship may differ significantly between species. It is therefore essential for any study of bet-hedging to include an examination of the effects of egg size in the particular species being considered.

The most commonly cited example in support of bet-hedging in frogs is a study by Crump (1981) which compared egg size distributions of five species from the Amazon Basin of Ecuador. When she compared egg-size distribution of clutches deposited in a temporary and a permanent pond, Crump found that temporary-pond clutches exhibited a trend towards platykurtosis while permanent-pond clutches exhibited more leptokurtic size distributions. This was interpreted as evidence for bet-hedging in response to environmental uncertainty in the temporary pond, and for the occurrence of stronger selection for some optimal value in the more stable permanent pond. However, closer inspection reveals that this interpretation rested on a rather tentative base. The actual distributions of all 7 clutches from the temporary pond were not significantly different from normal, and of the 7 clutches from the permanent pond, only one was significantly leptokurtic, while one was significantly skewed to the left, one was significantly skewed to the right, and the remaining four were not significantly different from normal. Furthermore, there was no significant difference in the amount of intraclutch variability in egg size between temporary-pond and permanent-pond breeders as measured by the coefficient of variation (CV). Crump admits that her sample sizes were rather small, and suggests that larger sample sizes might have produced more convincing evidence. In addition, her argument could have been strengthened by an investigation of the effects of egg size on larval fitness in the species she studied.

Another study that demonstrated a positive correlation between ICV and environmental unpredictability was conducted by Lips (2001), in Costa Rica. She found that in *Hyla calypsa*, ICV was highest at the beginning and end of the wet season, when rainfall was most intermittent. This species lays eggs on the underside of leaves overhanging mountain streams, where they develop for about 60 days before hatching and dropping into the water (Lips 2001). Rainfall is essential to keep the eggs hydrated, and desiccation is one of the main causes of egg mortality (Lips 2001). Lips found that the coefficient of variation of egg diameter varied across the wet season, with larger, more variable eggs produced both early and late in the season. Again, a follow-up study looking at the effects of egg size on susceptibility to desiccation would be required before Lips' bet-hedging hypothesis can be accepted with any confidence.

A study by Kaplan & King (1997) presents the only evidence so far to suggest that ICV in amphibians is not genetically determined (and thus that phenotypic differences are not a result of

genotypic differences). They found that individual *Bombina orientalis* females exhibit a high degree of variation in the size of offspring of sequential clutches deposited in the lab. Furthermore, in an 8-year field component of their study, mean egg size and ICV fluctuated among years and were correlated with environmentally induced shifts in parental body mass. The authors concluded that egg size is highly subject to non-genetic sources of variation.

Dziminski (2000) surveyed the incidence of ICV in various species of frogs living in a notoriously unpredictable environment, the Australian tropical savanna (Boulton & Brock 1999), and examined the consequences of egg size for larval ecology. He found that ICV in egg size occurs to varying degrees in all 15 species examined, being particularly high in species that breed in extremely ephemeral pools (e.g. burrowing frogs). The results of his larval growth experiments showed that larger eggs produce larger hatchlings, and that these size differences persist for a substantial fraction of the larval period. Finally, Dziminski looked at the effects of inter- and intra-specific competition on fitness of *Limnodynastes ornatus* larvae from different-sized eggs, and although none of the trends were statistically significant, he found there was a tendency for larvae from smaller eggs to be disadvantaged when experiencing density dependent interactions. Furthermore, under interspecific competition, both large and small larvae seemed to be more successful in mixed size treatments than when raised in uniform size treatments, which Dziminski suggested might have been due to behavioural avoidance or distinct microhabitat requirements, which reduced competition. Although he found a trend for higher ICV in certain species, more conclusive proof of bet-hedging would require demonstration of within-species correlations of ICV with environmental unpredictability.

CONCLUSION

Theory suggests that in a temporally variable and unpredictable environment, a parent may be able to increase the geometric mean fitness of its genotype by following a diversified bet-hedging strategy. Such bet-hedging strategies involve creating offspring with a range of phenotypes, so that whatever environmental conditions eventuate, some individuals will be well-suited. Two common forms of diversified bet-hedging in parental investment strategies are spreading reproductive effort over time by creating offspring with variable dormancy times, and by spreading offspring across an environment-specific fitness gradient, such as size. So far, there is very little conclusive evidence for bet-hedging, and the area requires many more carefully designed studies. Such studies must strive to test all the predictions of theory simultaneously, in order to rule out non-adaptive explanations for observed variation.

Introduction:

The establishment of dominance in male jewel skinks, *Carlia jarnoldae*: the roles of displays, body size and colouration

When two animals seek access to a limited resource, social conflict occurs (Hand, 1986; Parker, 1974). Both parties can benefit from settling social conflict without escalated fighting, as this can be costly in time and energy, can attract predators, and can result in injury or even death (Gould and Gould, 1989; Hand, 1986). Therefore, animals often use ritualised signals and displays to communicate with their opponents about the factors likely to determine the outcome of a fight – namely, fighting ability and motivation (Maynard Smith, 1974; McMann, 2000; Rohwer, 1982). In this way, escalated fights with a predictable outcome can be avoided, because an animal will usually retreat from an opponent who is much stronger or who is willing to pay a higher cost (McMann, 2000; Parker, 1974).

Once an animal has won access to a resource, it may continue to use signals and displays to help show at a distance that the resource is owned, and that the owner is prepared to fight for it (Butcher and Rohwer, 1989). Other animals should keep their distance, because the owner of a resource usually wins fights over it. This is because superior fighters tend to become owners in the first place, and because owners are more likely to escalate to a dangerous conflict level because the resource has greater value to them (Butcher and Rohwer, 1989; Krebs and Davies, 1993).

The signals and displays that animals use are extremely varied. Because body size is usually a strong predictor of fighting ability, signals used during contests are often designed to enhance assessment of body size. For example, male European toads, *Bufo bufo*, use the pitch of the croak to judge each other's body size, since larger males produce deeper croaks (Davies and Halliday, 1978). Other animals use visual displays to emphasise their body size, such as lateral orientations of the body, and raising of the fur, feathers or fins (Bradbury and Vehrencamp, 1998).

When animals use displays to signal ownership of resources such as territory, their signals are often designed to travel efficiently over longer distances. For example, birds sing within their territories to “broadcast” their presence to competitors (Catchpole and Slater, 1995; Nowicki et al., 1998). Studies have shown that transmission range in bird song is maximised by tailoring calls to the acoustic environment in which they are typically given (Morton, 1975). Similarly, many territorial lizards use head bob displays to signal territory ownership (Carpenter and Ferguson, 1977; Stamps, 1977). The amplitude and frequency of

these displays varies among species, possibly to maximise conspicuousness against motion patterns in the background vegetation, and to increase the distance over which they can be perceived by conspecifics (Fleishman, 1992).

Aggressive displays in many animals involve the exposure of bright colour patches. Such colour patches may provide information about the fighting ability of an individual, and they may enhance the distance over which displays can be perceived by the intended recipient. There is good experimental support that showy colouration can be important during male-male competition in birds (reviewed in Andersson, 1994). For example, in redwing blackbirds, *Agelaius phoeniceus*, males defend territories against other males during the breeding season by singing, displaying their red wing epaulets, and fighting. Larger males with brighter markings, bigger song repertoires and higher display rates secure bigger and better quality territories that attract more females. Experimental blackening of the bright red stripes on the wing had no effect on a male's ability to attract females, but did strongly reduce his ability to defend his territory, resulting in a sharp increase in territorial incursions by floater males and resident neighbours. These results suggest that the red epaulets of male redwing blackbirds function not in female choice, but in male-male competition. Males compete with each other for territories encompassing the best nesting sites, while females simply choose the best places to nest (Hansen & Rohwer, 1986; reviewed in (Gould and Gould, 1989).

Similarly, the size of the scarlet pectoral tuft of the scarlet-tufted malachite sunbird, *Nectarinia johnstoni*, seems to play an important role in male-male assessment during territorial disputes (Evans and Hatchwell, 1992). In this species, males display their pectoral tuft to other males during contests over territory. In manipulation experiments, males with reduced tuft size lost territory area, while males with enlarged tufts increased the size of their territories.

Many lizards also use display structures and signals to advertise their competitive abilities to opponents during contests (Carpenter and Ferguson, 1977; Cooper and Greenberg, 1992; Pough et al., 2001). A recent comparative study of display complexity in iguanid lizards suggests that intensity of male-male competition has been a significant factor in the evolution of complex signals in lizards (Ord et al., 2001). In many species, males develop brightly coloured patches on the body during the breeding season, the time when they frequently engage in contests, either directly over females, or over resources needed to attract females, such as territory (Cooper and Greenberg, 1992; Stamps, 1977). Many authors have suggested (Noble and Bradley, 1933), and several recent studies have shown (Olsson, 1994; Thompson and Moore, 1991) that male lizards use these badges to assess each other's fighting ability (reviewed in Pough et al., 2001).

For example, in the tree lizard *Urosaurus ornatus*, males extend their colourful dewlap (throat fan) during aggressive encounters, and the size of the central blue area of the dewlap reflects male aggressiveness (Thompson and Moore, 1991). In experimental trials between pairs of males, individuals with blue areas that were either naturally larger or artificially enlarged with paint were dominant over males with smaller blue areas (Thompson and Moore, 1991).

Similarly, male Swedish sand lizards, *Lacerta agilis*, display their lateral green colouration during ritualised contests over access to individual females during the mating season (Olsson, 1994). The green colouration covers the sides of the body in all males, but to varying degrees, and it also varies in saturation. Both the area and saturation of the green patch correlate with body size, which is strongly related to fighting ability (Olsson, 1994). In paired contests between males that had their green patches enlarged or reduced with paint, males with larger green areas were more likely to initiate contests with and to win against males with smaller areas.

Although the use of displays and colouration has been well studied in some groups of lizards such as iguanids, teids and agamids (Carpenter and Ferguson, 1977; Ord et al., 2001; Stamps, 1977), little is known about social behaviour in skinks. Members of this family are generally considered to be cryptically coloured, secretive and fossorial (Cooper and Greenberg, 1992; Stamps, 1977), and to consequently lack territoriality (Stamps, 1977) or complex social behaviour (Done and Heatwole, 1977; Greer, 1989). Although this may be true of most skinks, in Australia this group includes species with bright sexually dimorphic colouration (Cogger, 2000; Greer, 1989), territorial defence (Greer, 1989; Jennings and Thompson, 1999), and complex social display behaviours (Langkilde et al., in press; Whittier and Martin, 1992). The few studies of social behaviour in Australian skinks suggest that intraspecific aggression varies widely in importance, from species that lack it completely (*Ctenotus robustus*, Done and Heatwole, 1977), through those that use ritualised displays to settle conflicts (*Eulamprus quoyi*, Done and Heatwole, 1977; *Carlia rostralis*, Whittier and Martin, 1992; *Lampropholis guichenotti*, Torr and Shine, 1996), to those that exhibit overt aggression in the form of fights and chases (*Cryptoblepharus virgatus*, Rankin, 1973; *E. kosciuskoi*, Done and Heatwole, 1977; *Tiliqui casaurinae*, Mebs, 1974 in Done and Heatwole, 1977; *Tiliqua gerrardii*, Stephenson, 1977, *Ctenotus fallens*, Jennings and Thompson, 1999).

The jewel skink (*Carlia jarnoldae*) of North-Eastern Australia appears to thoroughly contradict the stereotypical image of skinks. It exhibits striking sexual colour dimorphism, with males possessing bright blue dorso-lateral spots and developing bright orange flanks and blue-green throats during the summer breeding season, while females remain cryptic brown. Furthermore, recent work suggests that members of this species are highly social and

use a wide array of display behaviours to communicate with conspecifics (Langkilde et al., in press). Finally, mark-recapture data suggest that males are territorial, defending their home ranges from other males, but overlapping with the home ranges of females (L. Schwarzkopf, unpubl. data.). Thus, *C. jarnoldae* represents an opportunity to expand understanding of the importance of colouration and displays in an understudied taxon, skinks.

I observed the social behaviour of male *C. jarnoldae* during paired contests in order to investigate the importance of display behaviours and colouration during the establishment of dominance in this species. My specific aims were to:

1. Describe the social behaviour of male jewel skinks during paired contests.
2. Describe how the lizards' behaviour changes over time, from when they first encounter one another to after a stable dominance relationship has been established.
3. Determine how the behaviour of dominant and subordinate individuals differs, and whether dominants are active over a greater area, or receive priority of access to important resources such shelter and basking sites.
4. Examine whether the lizards choose to display in particular environmental contexts, such as different substrates, levels of light and location, which might maximise the conspicuousness of their displays.
5. Examine whether certain physical traits - body size, colour (hue, value or chroma) of the flank, throat or spots, or the size of the orange flank patch - are associated with dominance in male jewel skinks, and whether any of these appear to function as cues to fighting ability.
6. Test the predictions of the "sequential assessment game" (Enquist and Leimar, 1983) that contests should be more escalated and costly when opponents are more closely matched in body size, colour, or size of the orange patch.

Display behaviours and the establishment of dominance in male jewel skinks, *Carlia jarnoldae*

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SUMMARY

During the establishment of social relationships, individuals use displays to communicate. The social and physical contexts in which displays are used determine their effectiveness. Here we examined the social and physical contexts of displays used during the establishment of dominance in experimentally paired male jewel skinks, *Carlia jarnoldae*. In our experimental enclosures, the lizards almost always (26/33) formed dominant-subordinate relationships within the first 48 hours of contact. Head bobbing and tail waving appear to be important means of opponent assessment in this species, as lizards spent more time engaging in these displays when they first interacted than a day later. Dominants displayed significantly more than subordinates on both days. Dominants also used the centre of the tank more than outer areas, thereby receiving priority of access to a wooden shelter. There was no decrease in levels of contest escalation and displays involving the exposure of colour patches over time, suggesting that individuals were still threatening each other after 48 hours of contact. Thus, escalation did not decrease even after reliable cues to contest outcome were available, suggesting that males of this species will not tolerate intruders in their territory. The lizards displayed most in environmental contexts that maximised their conspicuousness, i.e., head bobs and tail waves both occurred more often on a raised platform and in the sun, whereas tail waving, which is the most conspicuous behaviour, also occurred frequently on the flat sandy substrate of the enclosures. Displaying on raised surfaces and in the sun probably enhances the efficiency of communication of specific displays.

INTRODUCTION

Communication involves the provision of information by a sender to a receiver, to the benefit of both parties (Bradbury & Vehrencamp, 1998). The sender benefits by altering the probability that the receiver will respond in a certain way, while the receiver benefits by using the information to make a better decision about how it should respond (Bradbury & Vehrencamp, 1998). The vehicle that provides the information is called a 'signal', and may be a sound, smell, movement, or electrical impulse (Bradbury & Vehrencamp, 1998).

The use of signals can be vital to an individual's ability to achieve important tasks, such as attracting mates, threatening rivals, and deterring predators. However, signal

production can be costly. Signals may be perceived by unintended recipients such as predators, who may use the signal information to the signaller's detriment. Thus, signals are often optimised to increase transmission to intended recipients, while reducing their detectability to unintended receivers (Endler, 1992). In addition, signalling may involve high expenditure of energy, so signals should evolve to maximise the efficiency with which recipients can detect them within a given environment. Different social contexts and environments therefore favour different types of signals (Endler, 1992; Bradbury & Vehrencamp, 1998).

A major social context in which signals are important is intraspecific contests over resources. During contests, individuals of many species use specialised signals to communicate with opponents about the factors likely to determine their outcomes – namely, the relative fighting ability and motivation of each individual (Maynard Smith, 1974; Rohwer, 1982; McMann, 2000). By using such signals, contests can often be resolved without escalated fighting, because the “loser” should retreat as soon as he learns that his opponent is a better fighter, or that he is willing to pay a higher cost (Parker, 1974; McMann, 2000). This is likely to benefit both parties, since escalated fighting can be costly in time and energy, can attract predators, and can result in injury or even death (Hand, 1986; Gould & Gould, 1989).

Ritualised signals are not only used during initial contests over resources, but are also widely used to signal ownership status and warn away rivals once resources have been acquired. For example, many birds have complex song repertoires that they use to alert competitors of their territorial ownership status and warn them to keep away (Nowicki et al., 1998). These have been termed “broadcast” displays, because they broadcast the message to any nearby individuals that the area is occupied, and that intruding will not be tolerated (Catchpole & Slater, 1995).

Similarly, many iguanid lizards use “assertion” displays (Carpenter, 1967 in Stamps, 1977) to signal territorial ownership, performing these displays spontaneously as they move about their territory, even when no conspecifics are visible. These are thought to play a similar role to bird calls, threatening any competitors that enter the visual range that intruding is likely to be met with aggressive attack.

Most skinks are active foragers, spending much of their time on the ground or under leaf litter. Within this microhabitat, visibility is often poor, and most skinks rely more on chemical communication than on visual signals (Pough et al., 2001). Consequently, bright colouration (Cooper & Greenberg, 1992), and complex display behaviours (Stamps, 1977) are rare amongst skinks. Territoriality is also rare in this family (Stamps, 1977), apparently because poor visibility makes detection of intruders difficult.

However, the jewel skink, *Carlia jarnoldae*, of North-Eastern Australia appears to be an exception, showing striking sexual dimorphism in colouration. Males possess a series of bright blue dorso-lateral spots and develop bright orange flanks and blue-green throats during the summer breeding season, while females remain cryptic brown. In addition, recent work suggests that this species is highly social, using a large array of display behaviours during social interactions (Langkilde, 1999; Langkilde et al., in press). Mark-recapture data suggests that males are territorial, defending their home ranges from other males, but overlapping with the home ranges of females (L. Schwarzkopf, unpublished data). Thus, *C. jarnoldae* represents an exciting opportunity to expand upon the current understanding of signal use in an understudied group, skinks.

In this study, we investigated the social behaviour of male *C. jarnoldae*. During paired encounters, we determined whether pairs establish dominant-subordinate relationships, and examined how their use of displays and aggressive behaviour changes over time, whether dominants and subordinates differ in their behaviour, and whether individuals display in particular environmental contexts. Specifically, our aims were to:

1. Describe the types of aggressive behaviour and displays used by male *C. jarnoldae* during paired contests.
2. Describe how the lizards' behaviour changes over time as stable relationships emerge, determining whether displays and aggression are most important during the initial stages of contests.
3. Determine how the behaviour of dominant and subordinate individuals differs, and whether dominants use certain behaviours to signal status, or receive priority of access to important resources such as shelter and basking sites, or a greater activity range.
4. Examine whether the lizards appear to select environmental contexts that maximise the conspicuousness of their visual displays, including substrates, levels of light, and location.

METHODS

Adult male *C. jarnoldae* were captured by hand from Campus Creek on the James Cook University campus (19°19'N, 146°45'E) in Townsville, Australia, between late January and early April 2003. Only healthy individuals with no external signs of parasite infestation were used.

Lizards were assigned to pairs opportunistically. Partners were randomly marked with either one or two small dots of white correction pen (Pentel CO. LTD., Fine Point Correction Pen, Tokyo Japan) on top of the head and snout, taking care to avoid the parietal

eye. This allowed them to be easily identified from a distance, and did not appear to cause any changes in their behaviour. A previous study of behaviour in *C. jarnoldae* found that similar markings made with coloured nail polish did not influence the lizards' behaviour (Langkilde, 1999).

We were unable to catch enough lizards to use each individual in only one trial, so some lizards (n=18) were used in two trials. During their second trials, lizards were placed into a new enclosure with a new opponent for whom this was also a second trial. Dominance status of individuals in their first and second trials was not significantly related (Fisher's Exact Test, Fisher statistic=3.228, p=0.2321, n=16).

At the conclusion of each trial, individuals were examined for fresh bite wounds. All lizards were eventually individually toe-clipped and released at the site of capture.

Enclosures

Trials were conducted in four large (220 x 110 x 52cm) oval, semi-natural outdoor enclosures. Each enclosure could be divided into two equal halves by a removable plastic partition painted grey to match the walls of the enclosure. Enclosures were situated within 1km of the site from which lizards were obtained, and received direct natural sunlight between approximately 0700 hrs and 1830 hrs each day. Each enclosure had a lid consisting of a light poly-tube frame supporting a combination of 50% and 80% shade cloth, which was propped up approximately 50cm on one side. This ensured that a variety of shade densities were available within the enclosures. A strip of galvanised metal flashing surrounded the top rim of the enclosure and extended approximately 10cm inwards, preventing lizards from escaping. The substrate was sand with a sparse covering of leaf litter. Food was available in the form of invertebrates that entered the open tanks, and was supplemented approximately every three days by live mealworms (*Tenebrio molitor* larvae) and crickets (*Acheta domestica*). Water was available *ad libitum* from a plastic tub (30 x 20 x 10cm) sunk into the substrate at each end of the enclosure. Each water tub contained at least one emergent rock, facilitating easy access to water and providing raised basking and display sites. In addition, each half of each enclosure was provided with a wooden shelter (35 x 26 x 4cm) placed adjacent to the removable partition. This provided a retreat site, and served as a raised platform for basking and displaying.

Each pair was randomly assigned to one of the enclosures, and each individual was randomly allocated to one side of the partition. Both individuals were placed into the enclosure at the same time, at least 36 hours before the first observation took place. This period allowed individuals to recover from any stress caused by capture and handling, to explore their surroundings, and to begin establishing a territory.

Thirty-five minutes before the first observation took place, the partition and the two wooden shelters were removed, and a smaller wooden shelter (24 x 14cm) was placed into the centre of the enclosure. The lizards were then left to recover from the disturbance and to begin interacting with each other.

Behavioural Observations

Lizards were observed from behind a freestanding opaque blind at the western end of each enclosure. Blinds were never moved during the experimental period. Five minutes before the first observation began, the observer quietly moved into position behind the blind and began watching the lizards. This allowed the animals to habituate to the presence of the observer and continue with normal behaviour.

Observations were made between 0730 hrs and 1100 hrs, the period when lizards are most active in the wild (Langkilde, 1999). A few exceptions occurred when morning observations were prevented by rain, and in these cases, observations were made as soon as possible after rain had ceased, but never after 1400 hrs.

Initially, pairs were observed for four days (n=11). However, as it became apparent that dominance relationships were almost always established and stable by the second day, observations were restricted to two days for subsequent (n=22) trials.

Both lizards in a pair were observed for 15 minutes each per day, providing a total of 30 minutes of observation time per pair, per day. The order in which individuals were observed was random, and the second observation was made immediately after the first. If a lizard was not visible (i.e., hiding under the shelter or under leaves) on the first observation attempt, the observer returned every 30 min until he had emerged.

The observations were recorded using a custom-written event-recording program on a Hewlett Packard 200LX palmtop computer. The start and end times of all behaviours performed by the individual being observed (hereafter known as the 'focal' animal) were recorded continuously in units of seconds past midnight, allowing the frequency and duration of each behaviour to be determined. In order to record the location of the animals, the enclosure was visually divided both lengthwise and widthwise into thirds, forming nine sectors of approximately equal area. Small marks on the inside walls of the enclosures were used as visual reference points to enable the location of the lizard to be accurately assessed. The location (sector), substrate ('sand', 'rock', 'on shelter', 'half on shelter', 'under shelter', 'half under shelter') and light level ('full sun', 'partial shade', 'full shade') of the focal animal were also recorded continuously. The behaviour and location of the second individual (hereafter known as the 'stimulus' animal), and descriptions of any interactions that occurred, were recorded using the program's note-taking function.

All areas of the enclosure were visible through the blind, except for a small area directly in front of the blind. If at any time the focal animal could not be seen, and was not known to be under the shelter, his behaviour was recorded as 'can't see'. If possible, observations were continued until 15 minutes of visible behaviour had been recorded.

Determining Dominance

We defined dominance as the ability to win at points of conflict (Hand, 1986). Thus, we identified dominant and subordinate individuals by comparing the number of interactions they won and lost during the combined observation periods of each pair on each day. An 'interaction' was defined as any incident where one individual moved to within 50cm of his opponent in a deliberate manner, and ended when one lizard (the 'loser') moved away. An individual was considered 'dominant' if he won a majority of interactions, while his opponent was considered 'subordinate'. If both individuals won an equal number of interactions, they were considered 'equal'. If fewer than two interactions were observed, the relationship was classed as 'unknown', since it was impossible to determine the relationship between the lizards.

Because most pairs had established stable dominant-subordinate relationships by day 2, the dominance score calculated for day 2 was used as the final dominance score for each individual, except when observations could not be made on day 2, and the dominance score from day 1 was used (n=3 pairs).

Behavioural Data Analysis

Each type of behaviour used by the lizards was classified as either 'shallow' or 'deep' depending on whether it occurred 'over' other behaviours. For example, behaviours such as 'head turn' and 'tail wave' were classed as shallow behaviours, because they occurred over other behaviours such as basking or crawling. In contrast, behaviours such as 'bask normal' and 'crawl' were classed as deep, since they represent underlying behaviours.

For each 15 min observation, the behaviour of the focal animal was quantified by calculating the rate (number per minute of observation time) of all shallow behaviours, and the duration spent doing (percentage of the observation period) all deep behaviours and most shallow behaviours (i.e., all but very rapid shallow behaviours such as head turn and tongue flick). Only behaviours performed by at least 10% of individuals were included in statistical analyses of behaviour.

An index of space use was generated by calculating the number of sectors (max.=9) the lizard entered at least once during the observation period, and an index of movement was

generated by calculating the number of sectors the lizard entered per minute of observation time.

We also calculated the proportion of time the focal individual spent: on each substrate (sand, rock, on shelter, half on shelter, under shelter, half under shelter); in each light level (full shade, partial shade, full sun); and in each major section of the enclosure (when the 9 sectors were pooled into three equal-sized sections, representing the end in which the lizard was initially held, the end in which his opponent was initially held, and the centre – “own side”, “partner’s side” and “centre”, respectively).

Changes in Behaviour Over Time

To see how the lizards’ behaviour changed from when they first encountered one another to after a dominance relationship had been formed, we compared the behaviour of individuals on days 1 and 2. Only individuals that we had been able to observe on both days (n=43) were included in the analysis.

We also tested whether contest behaviour was more escalated on day 1 or day 2 in pairs that were observed on both days (n=25). Escalation in each pair on each day was quantified in four different ways: (1) the average number of interactions per 15 min, (2) the average number of ‘intense’ interactions per 15 min (defined as interactions in which the lizards were less than 20cm apart, or that ended in a chase), (3) the average value of an ‘escalation’ index, and (4) the maximum value of the ‘escalation’ index for that day. An index of escalation was generated for each 15 min observation period, and could take a value of 0 (meaning there was no interaction between opponents whatsoever), 1 (opponents displayed to each other, but did not interact directly), 2 (opponents had at least one interaction), or 3 (opponents had at least one intense interaction).

Overall differences between the behaviour of individuals and between the escalation of contests on the first and second days of the trial were tested using non-parametric, multivariate paired difference tests (“Multi-Response Permutation Procedure for Blocked Data”, hereafter referred to as MRBP, BLOSSOM version W2003.2). Four MRBP tests were performed: (1) rates of behaviours (head turn, tongue flick, mouth scrape, gape, head tilt, throat flash, distal third, tail wave, head bob, jump), (2) durations of display behaviours and postures (gape, head tilt, throat flash, distal third, tail wave, head bob, bask flat, bask normal, bask high, body lift, crawl & head bob, crawl & tail wave), (3) durations of movement behaviours (crawl, crawl & head turn, crawl & tongue flick, patrol, dart, run, approach, chase, flee, hang), and (4) measures of escalation (number of interactions, number of intense interactions, average escalation index, max. escalation index).

When multivariate tests indicated that there was a difference between days 1 and 2 for a group of variables, we determined which variables differed using Wilcoxon's Signed Ranks tests. We performed these tests at comparisonwise significance levels of $\alpha=0.05$, since the initial multivariate tests ensured an experimentwise Type I error rate of $\alpha=0.05$. This principle of hierarchical testing also applies to the other tests used throughout this paper.

Differences between Dominants & Subordinates

In order to compare the behaviour of dominant and subordinate lizards, we analysed the behaviour of lizards on day 2, when dominance relationships had been established. Only pairs in which both individuals were observed on day 2, and in which a clear dominant-subordinate relationship could be determined by day 2, were included in statistical analyses (n=19 pairs).

Five MRBP tests were used to test for overall differences between dominant and subordinate lizards in: (1) movement / space use indices (number of sectors entered per min, number of sectors used in total), (2) rates of behaviours (head turn, tongue flick, mouth scrape, gape, head tilt, throat flash, distal third, tail wave, head bob, jump), (3) durations of behaviours (gape, head tilt, throat flash, distal third, tail wave, head bob, bask flat, bask normal, bask high, body lift, crawl, crawl & head bob, crawl & tongue flick, patrol, dart, run, approach, chase, flee, hang), (4) duration spent on each substrate (sand, rock, on shelter, half on shelter, under shelter, half under shelter), and (5) duration spent in each section of the enclosure (own side, centre, partner's side).

For test groups in which a significant overall difference between dominants and subordinates was found, differences in individual variables were tested using Wilcoxon Signed Ranks tests. All tests were two-tailed, except for the behaviours 'chase' and 'flee', which were one-tailed, since we predicted *a priori* that dominant individuals would chase more and that subordinate individuals would flee more.

Behaviour Contexts

In order to test the null hypothesis that the lizards head bobbed or tail waved randomly with respect to substrate, we compared observed and expected rates and durations of these behaviours performed on each of the six substrates. We used data from individuals observed on day 1 (n=54), since lizards tended to display most on this day (see Fig. 1 in Results). Expected values were calculated by determining the proportion of observed display behaviours that would have occurred on each substrate if displays were performed at their

observed rates and durations without regard to substrate, and substrates were occupied at the observed rates.

Observed and expected values were compared using MRBP tests. Testing was done in a hierarchical fashion, the first test being an overall test including all variables (rates and durations of head bobs and tail waves on each of the six substrates, $n=24$ variables). If that test indicated a significant difference, rates ($n=12$ variables) and durations ($n=12$ variables) of head bobs and tail waves on each of the substrates were tested separately, without adjustment of the alpha level. Finally, if those tests still indicated a significant difference, separate tests on the rates ($n=6$ variables) and durations ($n=6$ variables) of behaviours on each substrate were conducted. As soon as a test indicated no significant difference, testing of those variables ceased, and was not continued at a finer scale. This hierarchical approach to hypothesis testing preserved our experimentwise error rate at $\alpha=0.05$ while allowing us to maximise the power of our multiple comparisons by using comparisonwise error rates of $\alpha=0.05$. The sequence of tests can be seen in Table 3 (Results).

We also tested whether lizards head bobbed, tail waved, throat flashed or head tilted randomly with respect to level of light, using only data from day 1, and only from observations when both sunny and shady areas were available within the enclosure ($n=24$). This was done using the same statistical methods as for substrates, above (and see Table 4, Results).

Finally, we examined environmental context-dependence for the behaviours mouth scrape, head bob and tail wave by determining whether these potentially territorial behaviours occurred at different rates in the lizards' own side, the centre, or the partner's side of the enclosure. Only data from day 1 were used ($n=52$), and statistical methods were the same as for substrates and enclosure sections, above (and see Table 5, Results).

RESULTS

A total of 33 trials were conducted using 48 lizards. By the second day of trials, 26 pairs had established a clear dominant-subordinate relationship, while five pairs appeared to be equal, and in the remaining two pairs the relationship could not be determined because opponents did not interact.

Aggressive Behaviour

Lizards usually exhibited overt aggression towards one another, engaging in both interactions (mean=1.86, range=0-7, $n=107$) and escalated interactions (mean=0.47, range=0-4, $n=107$) during the 15 min observation periods.

Aggressive interactions consisted of one individual approaching, either directly up to his opponent, or stopping along the way to perform display behaviours. They were settled most quickly when the individual being approached rapidly moved away from his aggressor (run, dart, or flee), or when the approaching individual “changed his mind” and turned back. However, if neither individual seemed willing to move away, a ‘face-off’ occurred, during which the lizards watched each other intently, sometimes from as close as 8cm. At this point, opponents often adopted raised postures and displayed to each other using head bobs, head tilts, and throat flashes. Interactions ended when either: (i) one or both of the lizards eventually crawled away and resumed normal activities such as patrolling and basking, (ii) one or both of the lizards suddenly fled, or (iii) one lizard suddenly lunged at the other, who always fled upon such provocation. When face-offs ended with a lunge, the winner often continued to chase the loser all around the enclosure.

Wrestling was never observed during the 42 hours of observation time. However, biting occurred during lunges and chases; 21.6% of individuals (9.1% of dominants and 30.4% of subordinates) exhibited fresh bite wounds on their bodies at the end of their trial. In one extreme case, the smaller lizard was found dead on the second day of his trial, with multiple large bite wounds on his body. Therefore, although they do not appear to wrestle, male *C. jarnoldae* certainly have the potential to cause each other serious harm.

Display Behaviours

Male *C. jarnoldae* used a wide range of display behaviours (head bob, tail wave, distal third tail wave, gape, throat flash, head tilt) and raised/tilted postures (bask high, body lift, lateral tilt) that exposed their lateral orange colouration. These behaviours of *Carlia jarnoldae* are described in a detailed ethogram, elsewhere (Langkilde et al., in press; and see Glossary). In general during our observations, raised postures and display behaviours were used most frequently during, or immediately after, interactions. However, some displays were used as lizards moved about the enclosure, whether or not the opponent was in view. For example, a common succession of behaviours to occur immediately after a burst of crawling was a head bob, followed immediately by a tail wave, followed by a less intense tail wave (distal third), during all of which the lizard basked high. In particular, tail waves (full and distal third) rarely occurred during interactions, but were frequently used by some individuals as they moved around. In contrast, head bobs and throat flashes were used commonly both during interactions and while moving around. In addition to displays, lizards also conducted a variety of maintenance behaviours such as foraging, basking, drinking and crawling.

Behaviours performed by fewer than 10% of individuals and therefore excluded from statistical analyses were lateral tilt, crawl & tail wave, and cloaca drag.

Changes in Behaviour Over Time

There was a significant overall difference between the first and second day in the duration the lizards spent doing display behaviours and postures, but not in rates of behaviours, or durations of movement behaviours (Table 1). There was no significant difference in escalation between days 1 and 2 (Table 1).

When display behaviour and posture duration variables were analysed individually, there were no significant differences between days 1 and 2 (Table 1). Only duration of head bobs ($z=-1.786$, $p=0.074$) and tail waves ($z=-1.823$, $p=0.068$) approach significance. Mean duration spent head bobbing and tail waving was longer on the first day in both cases (Fig. 1). Although statistical tests could only be performed on days 1 and 2 due to sample size limitations, data from days 3 and 4 are included in the graphs for visual assessment. As can be seen in the figures, both head bobs and tail waves were done for longest on day 1.

Comparison of Dominants & Subordinates

There were significant overall differences between dominant and subordinate lizards in their rates of behaviour, durations of behaviours, durations spent on each substrate, and duration spent in each section of the enclosure, but not in their space use or movement (Table 2). A number of specific differences between dominant and subordinate lizards were found when variables were analysed individually (Table 2).

Dominants displayed much more frequently than subordinates, doing significantly more head bobs, head tilts, and distal third and full tail waves (Fig. 2). Dominants also did more throat flashes (although not significantly so), but dominants and subordinates differed little in the rate at which they performed gapes (Fig. 2). Dominant lizards also head turned and tongue flicked at significantly higher rates than subordinates did (Fig. 2). Both dominants and subordinates mouth scraped, but dominants tended to do so more frequently than subordinates did (Fig. 2). Finally, dominants and subordinates differed little in the number of times they jumped up the enclosure walls (Fig. 2).

Dominants spent significantly more time head bobbing and tail waving (both distal third and full tail waves), however, although they head tilted more frequently than subordinates (Fig. 2), they did not spend more time head tilting (Fig. 3). This suggests that dominants did a greater number of more rapid head tilts than subordinates. Dominants and subordinates differed little in the amount of time they spent doing gapes (Fig. 3).

Table 1: Comparisons of behaviour and contest escalation of paired male *C. jarnoldae* between days 1 and 2, using non-parametric multivariate paired difference tests and Wilcoxon's Signed Ranks tests.

Overall Test Group	Overall Test Result	Variables	Wilcoxon Z value	P value	1- or 2-tailed
Rates of behaviours	$\delta = -1.6205$ P = 0.0713	head turn	-	-	-
		tongue flick	-	-	-
		mouth scrape	-	-	-
		head tilt	-	-	-
		throat flash	-	-	-
		distal third	-	-	-
		tail wave	-	-	-
		head bob	-	-	-
		gape	-	-	-
		jump	-	-	-
Durations of display behaviours & postures	$\delta = -1.9970$ P = 0.0383	gape	-1.069	0.285	2
		head tilt	-1.109	0.267	2
		throat flash	-1.547	0.122	2
		distal third	-0.150	0.881	2
		tail wave	-1.823	0.068	2
		head bob	-1.786	0.074	2
		bask flat	-0.776	0.438	2
		bask normal	-0.394	0.694	2
		bask high	-0.473	0.636	2
		body lift	-0.631	0.528	2
		crawl & head bob	-1.448	0.148	2
		crawl & tail wave	-1.183	0.237	2
Durations of movement behaviours	$\delta = -0.07531$ P = 0.2070	crawl	-	-	-
		crawl & head turn	-	-	-
		crawl & tongue flick	-	-	-
		patrol	-	-	-
		dart	-	-	-
		run	-	-	-
		approach	-	-	-
		chase	-	-	-
		flee	-	-	-
		hang	-	-	-
Escalation	$\delta = 0.2200$ P = 0.4587	no. interactions	-	-	-
		no. intense interactions	-	-	-
		'escalation' (avg.)	-	-	-
		'escalation' (max.)	-	-	-

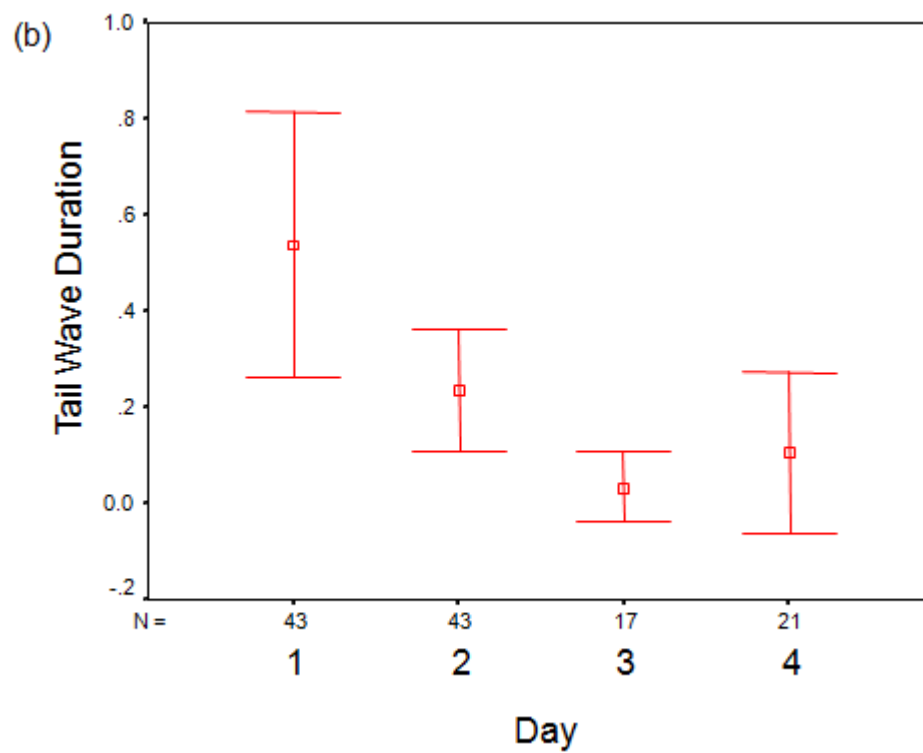
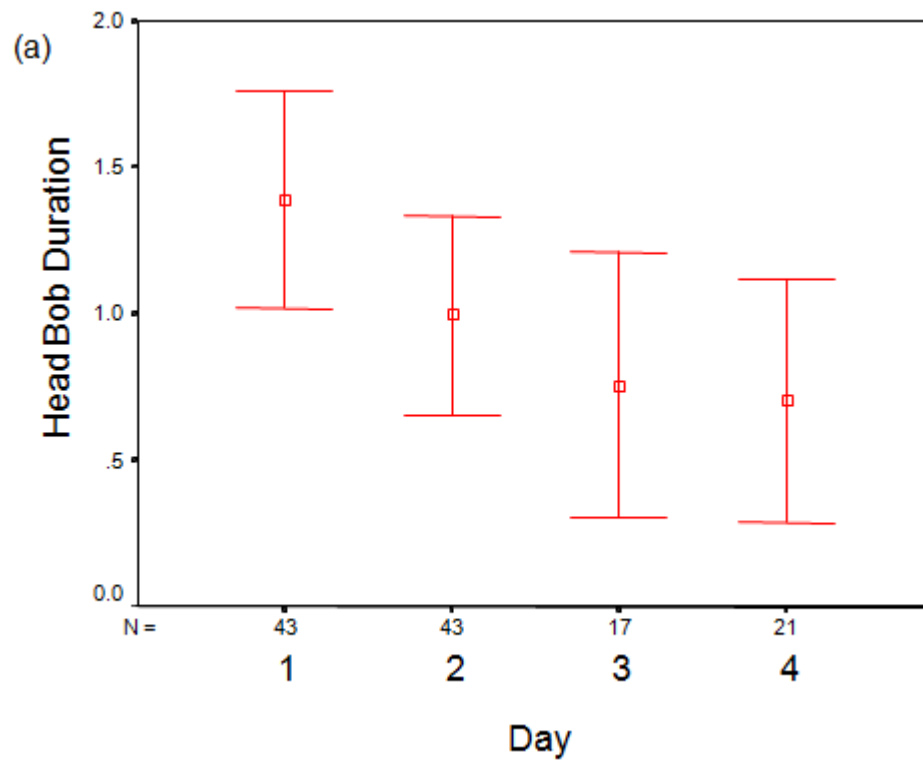


Fig. 1: Mean (\pm 95% CI) duration spent (a) head bobbing and (b) tail waving on each day.

Table 2: Comparisons of behaviour of dominant and subordinate individuals, using non-parametric multivariate paired difference tests and Wilcoxon's Signed Ranks tests.

Overall Test Group	Overall Test Result	Variables	Wilcoxon Z value	P value	1- or 2-tailed
Space use / movement	$\delta = 1.0086$ P = 0.9469	no. sectors used	-	-	-
		movement index	-	-	-
Rates of behaviours	$\delta = -7.4149$ P = 7.67 E-05	head turn	-3.3	0.001	2
		tongue flick	-3.3	0.001	2
		mouth scrape	-1.407	0.159	2
		head tilt	-2.614	0.009	2
		throat flash	-1.175	0.240	2
		distal third	-3.171	0.002	2
		tail wave	-3.237	0.001	2
		head bob	-3.34	0.001	2
		gape	-0.368	0.713	2
		jump	-1.001	0.317	2
Durations of behaviours	$\delta = -6.2444$ P = 6.82 E-05	head tilt	-0.327	0.744	2
		throat flash	-1.784	0.074	2
		distal third	-3.171	0.002	2
		tail wave	-3.234	0.001	2
		head bob	-3.099	0.002	2
		bask flat	-1.489	0.136	2
		bask high	-3.018	0.003	2
		bask normal	-0.04	0.968	2
		body lift	-2.547	0.011	2
		crawl	-2.495	0.013	2
		crawl & head bob	-0.73	0.465	2
		crawl & tongue flick	-2.173	0.030	2
		patrol	-1.728	0.084	2
		run	-2.556	0.011	2
		approach	-2.803	0.005	2
		chase	-1.826	0.034	1
		flee	-1.718	0.043	1
hang	-0.664	0.507	2		
gape	-0.365	0.715	2		
dart	-1.125	0.260	2		
Duration spent on each substrate	$\delta = -3.2647$ P = 0.0083	sand	-2.294	0.022	2
		rock	-1.287	0.198	2
		on shelter	-0.647	0.099	2
		half on shelter	-2.201	0.028	2
		under shelter	-2.023	0.043	2
		half under shelter	-2.023	0.043	2
Duration spent in each enclosure section	$\delta = -3.7152$ P = 0.0071	own side	-0.322	0.748	2
		centre	-2.857	0.004	2
		partner's side	-2.548	0.011	2

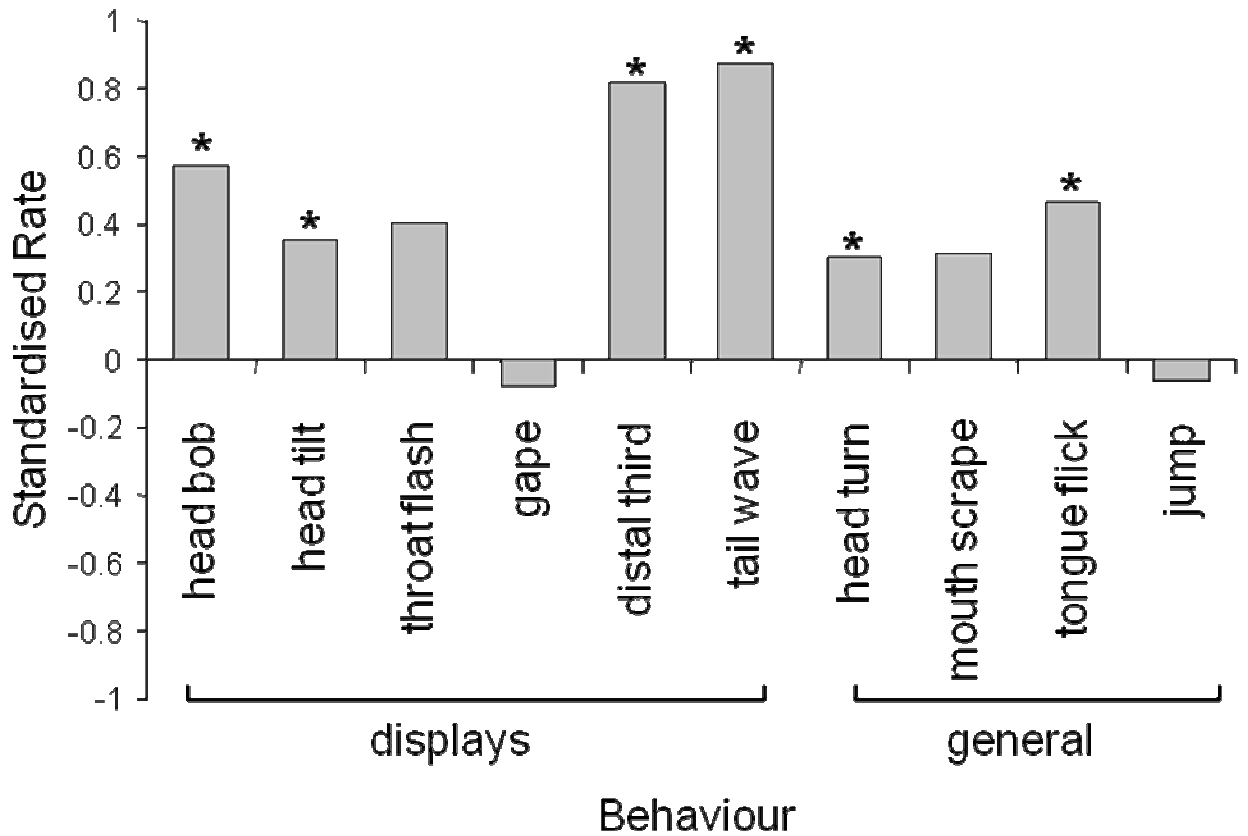


Fig. 2: Standardised difference between dominants and subordinates in rates of various displays and general behaviours. The value on the Y-axis is the mean value for dominants minus the mean value for subordinates, divided by the mean across all individuals. A value of 1 indicates that only dominant individuals ever did that behaviour, while a value of 0 means that dominants and subordinates did it equally, and a value of -1 indicates that only subordinates ever did it. Significant differences between dominants and subordinates are highlighted with a star.

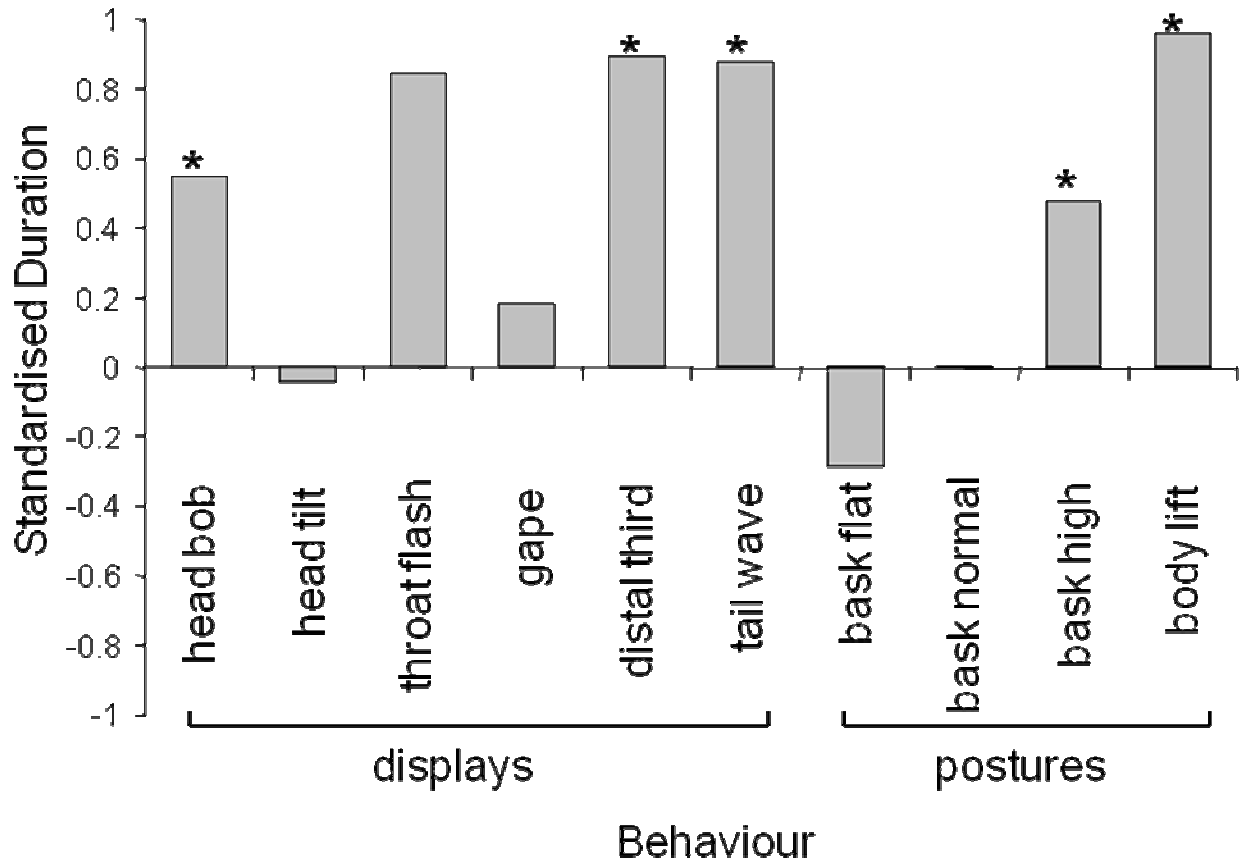


Fig. 3: Standardised difference between dominants and subordinates in duration spent doing various displays and postures. The value on the Y-axis is the mean value for dominants minus the mean value for subordinates, divided by the mean across all individuals. A value of 1 indicates that only dominant individuals ever did that behaviour, while a value of 0 means that dominants and subordinates did it equally, and a value of -1 indicates that only subordinates ever did it. Significant differences between dominants and subordinates are highlighted with a star.

Dominant and subordinate lizards also differed in the types of postures they used, with a trend for increasing elevation in posture with increasing status (Fig. 3). Dominants spent significantly more time in raised postures (bask high and body lift) (Fig. 3). In fact, subordinates almost never body lifted (note the height of the bar approaches 1). Subordinates tended to spend more time in a flattened posture (bask flat), and dominants and subordinates did not differ in the amount of time they spent basking normally (Fig. 3).

Some movement behaviours were directly involved in aggressive interactions, either by initiating (approach, chase) or terminating (run, dart, flee) them. Dominant lizards approached and chased significantly more than subordinates, who very rarely approached, and never chased their opponents (Fig. 4). Conversely, subordinate lizards spent significantly more time running and fleeing, and also tended to spend more time darting (Fig. 4).

Dominants moved around more than subordinates, spending significantly more time crawling and crawl & tongue flicking, and also tending to crawl & head bob more (Fig. 4). In contrast, subordinates tended to patrol and hang on the enclosure wall slightly more than dominants, suggesting they were trying to escape (Fig. 4).

Dominant and subordinate lizards not only differed in the types of behaviours they used, but also in the amount of time they spent on the different substrates. Dominants spent significantly more time half on, under, and half under the shelter, while subordinates spent significantly more time on the sand (Fig. 5). In fact, only dominants ever went half on, under or half under the shelter (Fig. 5).

There was no difference in the amount of time lizards spent on their own side of the enclosure, whereas dominants spent significantly more time in the centre, and subordinates spent significantly more time on their partner's side (Fig. 6). This happened because subordinates spent roughly equal amounts of time in each of the three sections, whereas dominants tended to spend longer in the centre than in either end (Fig. 7). Both dominants and subordinates spent slightly longer in their own side than in their partner's side, but because dominants spent so much longer in the centre, subordinates spent relatively more time in their partner's side than dominants did (Fig. 7).

Behaviour Contexts

Substrate. Rates and durations of head bobs and tail waves differed significantly from those expected on different substrates (Table 3), occurring more often on particular substrates (Fig. 8). The rates and durations of these behaviours showed almost identical patterns, therefore only durations are presented graphically. Lizards head bobbed for longer than expected both on and half under the shelter, but less than expected on the sand and

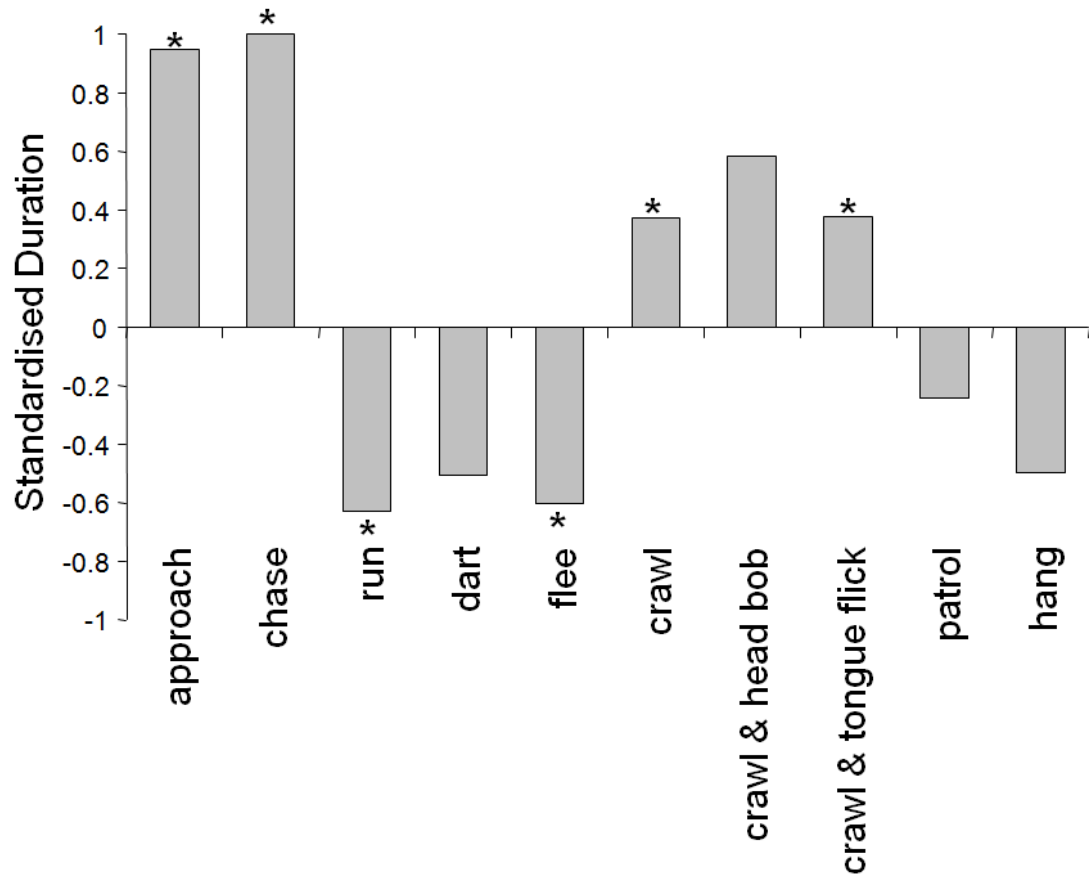


Fig. 4: Standardised difference between dominants and subordinates in duration spent doing various movement behaviours. The value on the Y-axis is the mean value for dominants minus the mean value for subordinates, divided by the mean across all individuals. A value of 1 indicates that only dominant individuals ever did that behaviour, while a value of 0 means that dominants and subordinates did it equally, and a value of -1 indicates that only subordinates ever did it. Significant differences between dominants and subordinates are highlighted with a star.

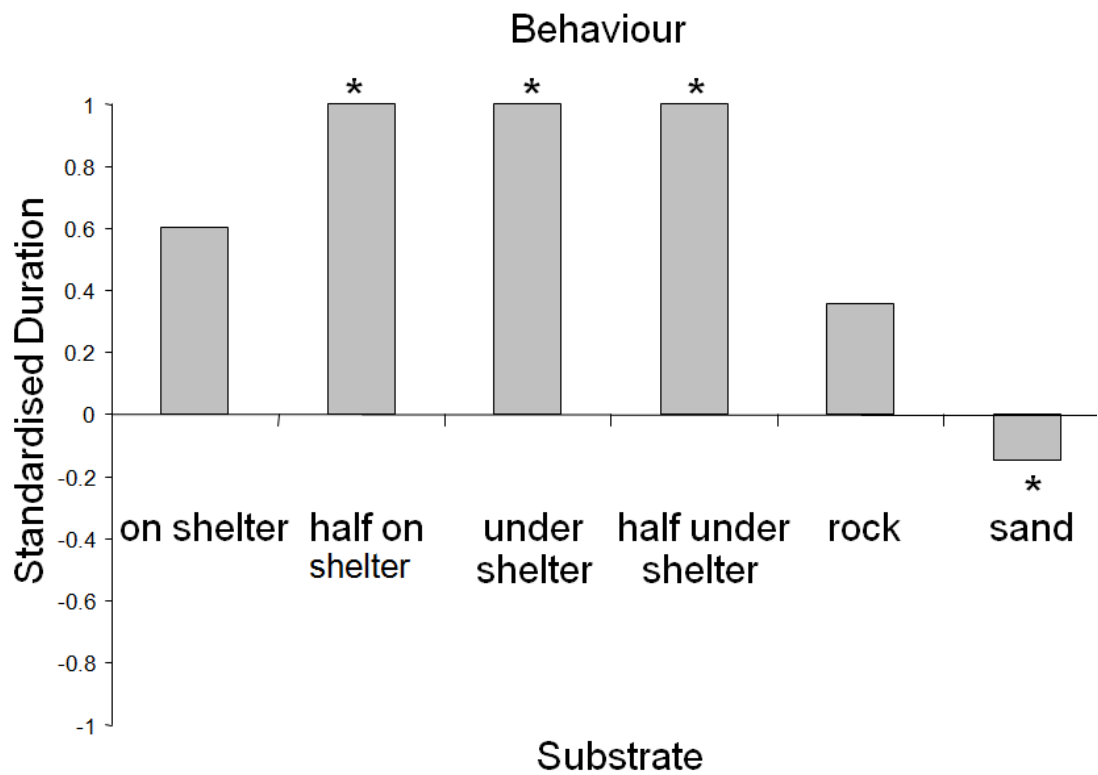


Fig. 5: Standardised difference between dominants and subordinates in duration spent on each substrate. The value on the Y-axis is the mean value for dominants minus the mean value for subordinates, divided by the mean across all individuals. A value of 1 indicates that only dominant individuals ever spent time on that substrate, while a value of 0 means that dominants and subordinates spent equal time on it, and a value of -1 indicates that only subordinates ever spent time on it. Significant differences between dominants and subordinates are highlighted with a star.

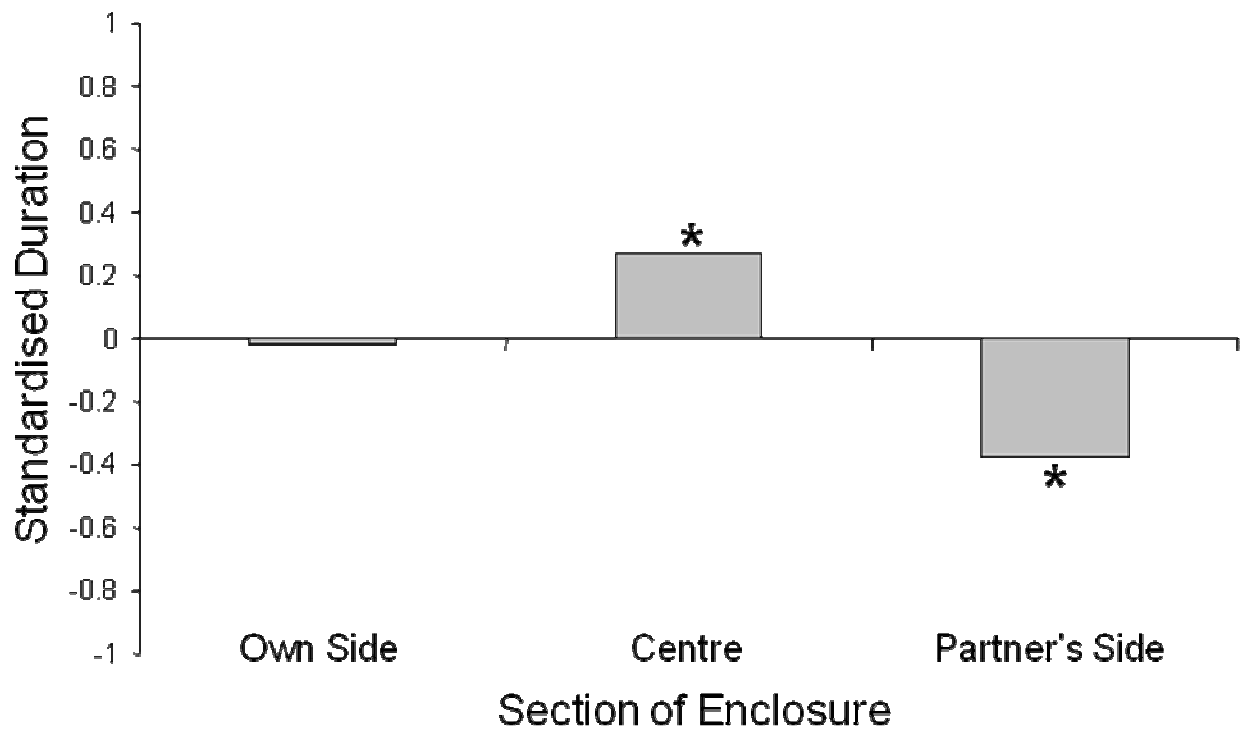


Fig. 6: Standardised difference between dominants and subordinates in duration spent in each section of the enclosure. The value on the Y-axis is the mean value for dominants minus the mean value for subordinates, divided by the mean across all individuals. A value of 1 indicates that only dominant individuals ever spent time in that section, while a value of 0 means that dominants and subordinates spent equal time in it, and a value of -1 indicates that only subordinates ever spent time in it. Significant differences between dominants and subordinates are highlighted with a star.

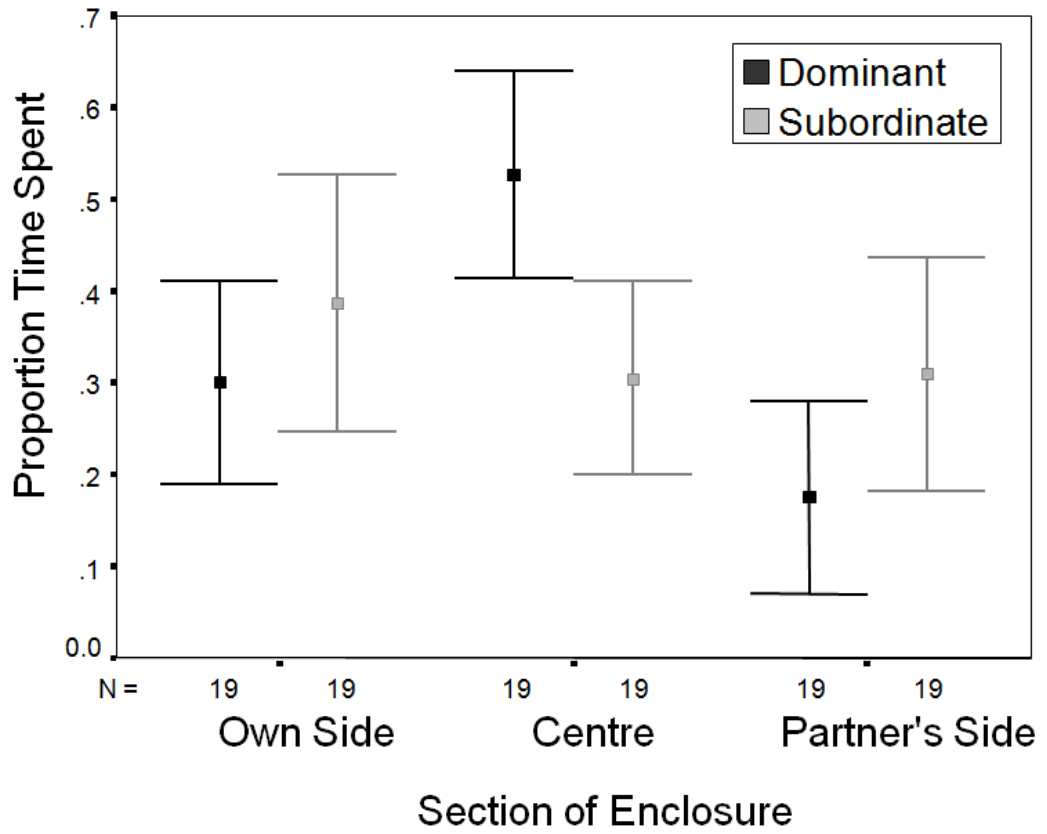


Fig. 7: Mean (\pm 95% CI) proportion of time dominants and subordinates spent in each section of the enclosure.

rocks (Fig. 8a). Duration of tail waving was far less than expected on rocks, but more than expected on sand and both on and half on the shelter (Fig. 8b).

Light. Amount of time spent head bobbing and tail waving were significantly non-random with respect to light level, but duration spent head tilting and throat flashing, and the rates at which all four behaviours were performed, were not (Table 4). Lizards clearly spent more time head bobbing and tail waving in the sun than in the shade or partial shade (Fig. 9).

Location. There were significant differences between observed and expected rates and durations of head bobs and tail waves performed in different sections of the enclosure (see Table 5), indicating that these behaviours did not occur randomly with respect to location (Fig. 10). The rates of these behaviours showed almost identical patterns, and are therefore not presented graphically.

Dominant lizards head bobbed and tail waved for much longer in the centre of the enclosure than at either end (Fig. 10). In contrast, subordinate lizards appear to have displayed randomly with respect to enclosure section, although there was a slight trend for head bobs to be longer in their own side than in their partner's side (Fig. 10).

DISCUSSION

In contrast to the usual concept of skink behaviour (Stamps, 1977), male *C. jarnoldae* are very social skinks, readily interacting with one other and using a wide repertoire of display behaviours and raised postures to signal to each other. These skinks almost always form dominant-subordinate relationships within the first 48 hours of contact, and display behaviours appear to play an important role in this process, both during initial assessment of opponents, and in the ongoing reinforcement of dominance status. Males displayed most often in certain environmental contexts.

Changes in Behaviour Over Time

Because ritualised displays and aggressive behaviour are often used during the establishment of dominance relationships, the frequency with which these behaviours occur is usually high when unfamiliar competitors first meet, but tends to decrease after stable dominance relationships have formed. For example, in many species that are seasonally territorial, aggressive interactions are most frequent and vigorous during the settlement period, but agonistic behaviour declines after territories have been established (lizards: Stamps & Krishnan, 1997; butterflies: Wickman & Wicklund, 1983; fish: van den Assem & van der Molen, 1969; birds: Gwinner et al., 1994; Ezaki, 1995).

Table 3: Hierarchical non-parametric multivariate paired difference tests comparing observed and expected rates and durations of behaviours on different substrates.

Variables Included in Test	Test Results	
head bob rate x substrates*	$\delta = -4.7091$ $P = \mathbf{0.0002}$	$\delta = -4.6836$ $P = \mathbf{0.0003}$
tail wave rate x substrates	$\delta = -5.0870$ $P = \mathbf{8.07 E-05}$	$\delta = -3.2630$ $P = \mathbf{0.0039}$
head bob duration x substrates		$\delta = -5.4220$ $P = \mathbf{0.0001}$
tail wave duration x substrates	$\delta = -5.1874$ $P = \mathbf{6.84 E-05}$	$\delta = -3.2211$ $P = \mathbf{0.0044}$

*substrates = sand, rock, on shelter, half on shelter, under shelter, half under shelter

Table 4: Hierarchical non-parametric multivariate paired difference tests comparing observed and expected rates and durations of behaviours under different light levels.

Variables Included in Test	Test Results	
head bob rate x light levels*		-
tail wave rate x light levels	$\delta = -1.0612$ $P = 0.1431$	-
head tilt rate x light levels		-
throat flash rate x light levels	$\delta = -3.2920$ $P = \mathbf{0.0045}$	-
tail wave duration x light levels		$\delta = -7.5530$ $P = \mathbf{6.80 E-05}$
head bob duration x light levels	$\delta = -4.2412$ $P = \mathbf{0.0005}$	$\delta = -2.5346$ $P = \mathbf{0.0257}$
head tilt duration x light levels		$\delta = 0.2069$ $P = 0.4826$
throat flash duration x light levels		$\delta = -1.4680$ $P = 0.0780$

*light levels = full shade, partial shade, full sun

Table 5: Hierarchical non-parametric multivariate paired difference tests comparing observed and expected rates and durations of behaviours in different enclosure sections.

Variables Included in Test		Test Results
head bob rate x enclosure sections		$\delta = -3.2921$ $P = \mathbf{0.0125}$
tail wave rate x enclosure sections	$\delta = -3.9188$ $P = \mathbf{0.0029}$	$\delta = -2.6427$ $P = \mathbf{0.0244}$
mouth scrape rate x enclosure sections	$\delta = -4.3089$ $P = \mathbf{0.0019}$	$\delta = -0.6804$ $P = 0.2102$
head bob duration x enclosure sections		$\delta = -2.7954$ $P = \mathbf{0.0212}$
tail wave duration x enclosure sections		$\delta = -3.5418$ $P = \mathbf{0.0080}$

*enclosure sections = own side, centre, partner's side

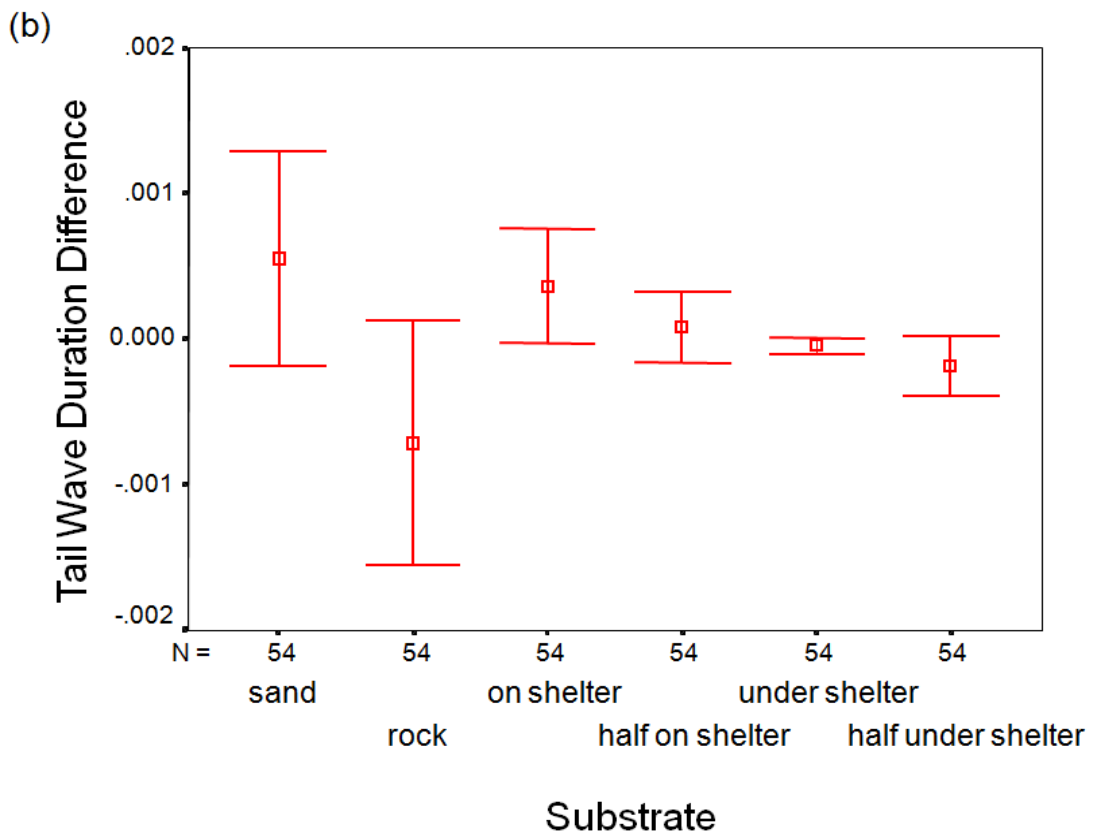
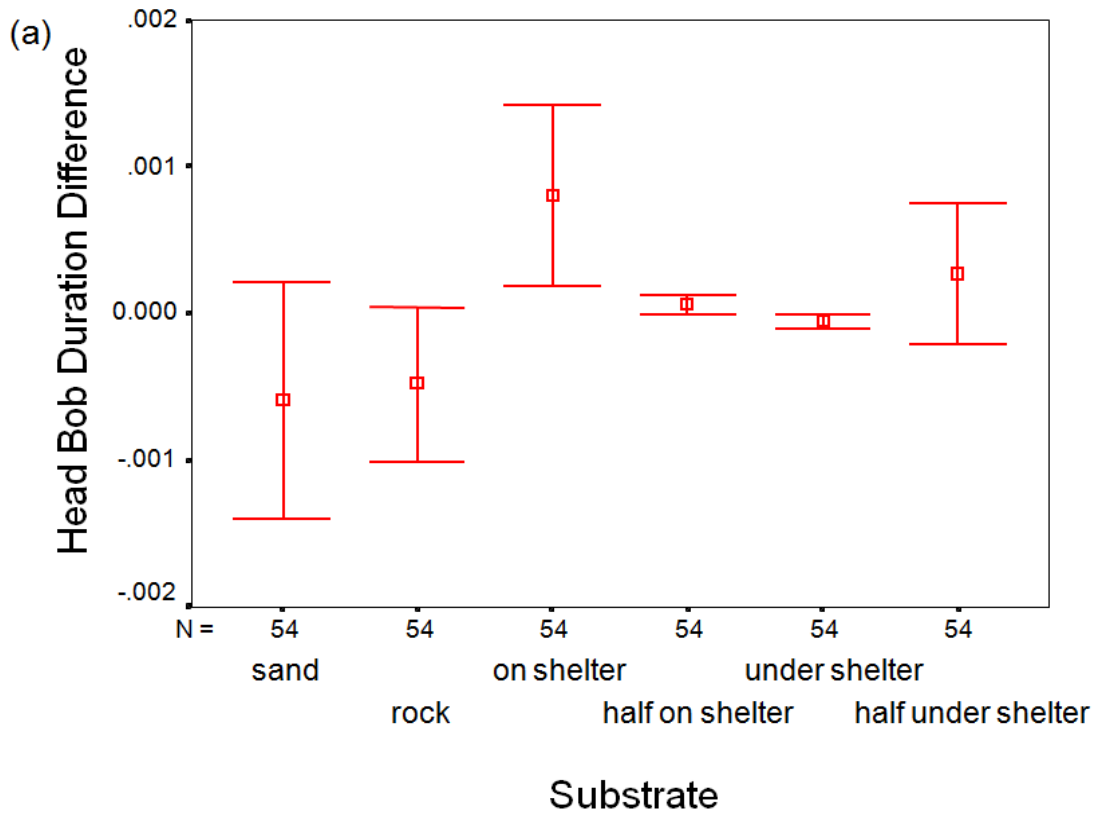


Fig. 8: Mean difference (\pm 95% CI) between observed and expected values of durations spent (a) head bobbing and (b) tail waving on different substrates.

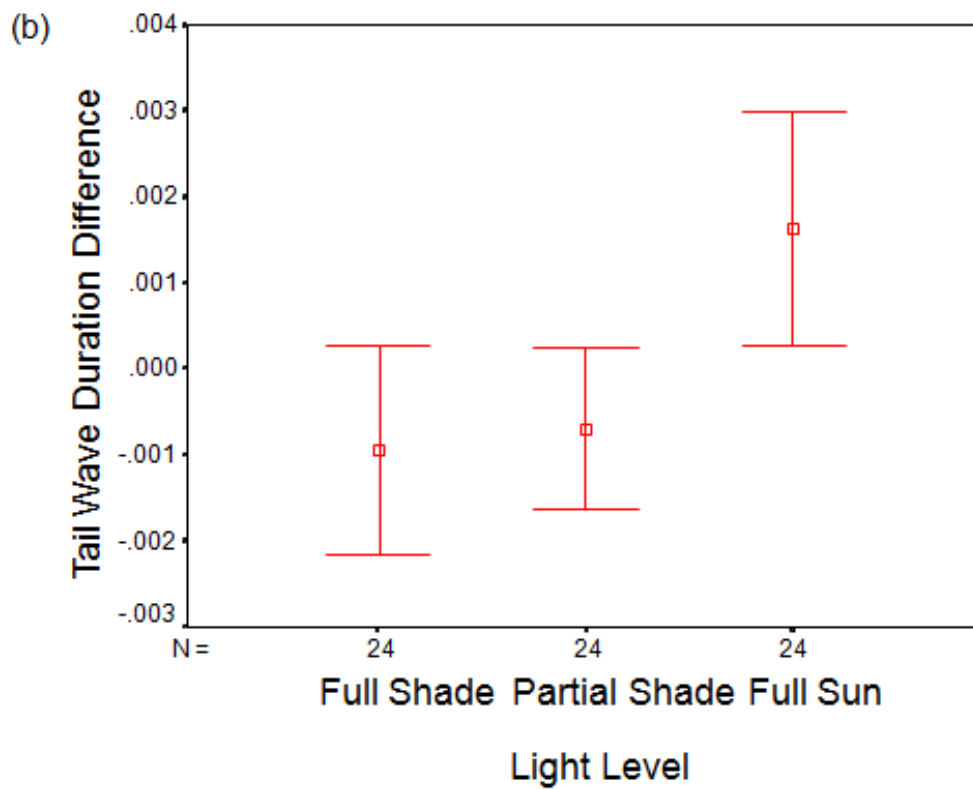
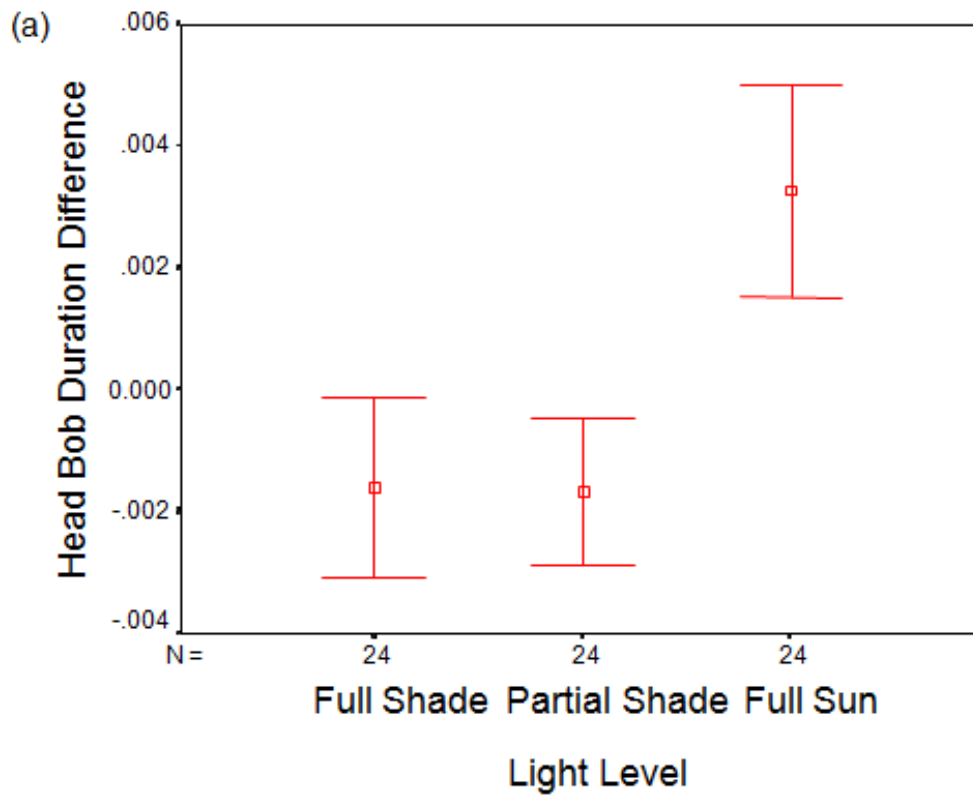


Fig. 9: Mean difference (\pm 95% CI) between observed and expected values of durations spent (a) head bobbing and (b) tail waving under different light levels.

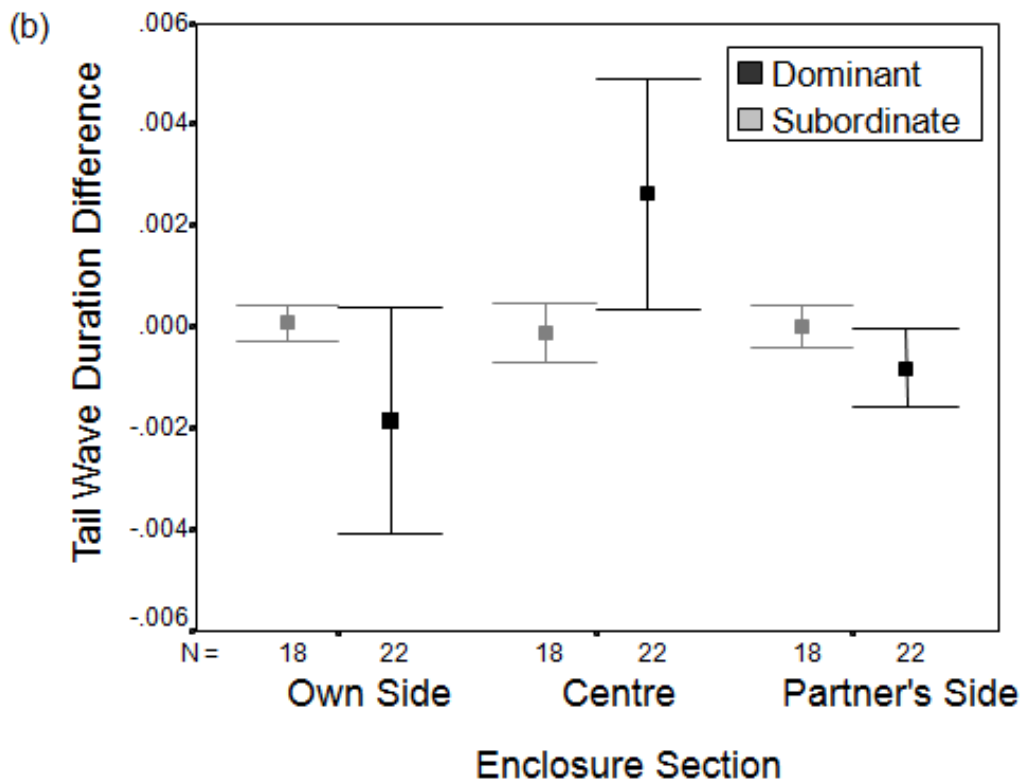
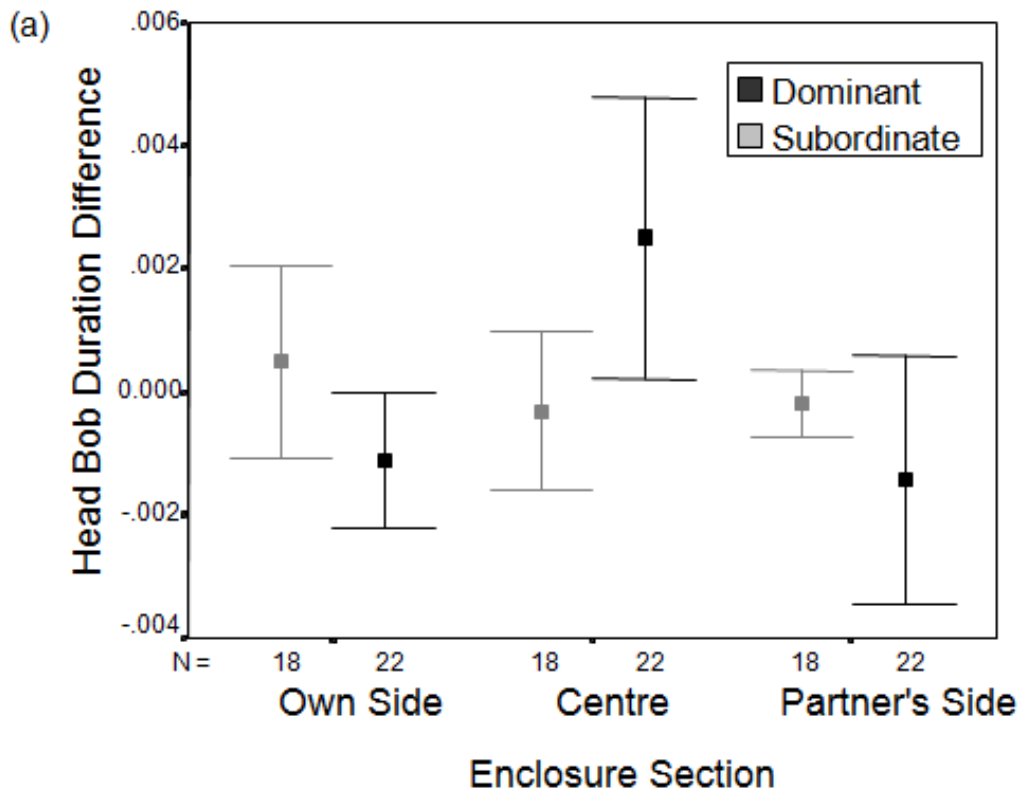


Fig. 10: Mean difference (\pm 95% CI) between observed and expected values of durations spent (a) head bobbing and (b) tail waving in different enclosure sections by dominant and subordinate individuals.

We found a significant overall difference between the first and second days of the trials in the amount of time male *C. jarnoldae* spent using display behaviours and postures. Although none of the multiple-comparisons tests for differences in individual behaviours were significant, the lizards tended to spend more time head bobbing and tail waving on day 1, suggesting that these behaviours are important means of communication between unfamiliar individuals during the establishment of dominance in this species. However, the lizards did not alter the amount of time they spent doing behaviours such as raised postures and throat flashes, which expose their distinctive colouration. Similar colour-exposing behaviours in the closely related skink *C. rostralis* may allow males to assess each other, as colouration provides information about the sex, reproductive status and age of individuals (Whittier & Martin, 1992). We observed that raised postures and throat flashes in *C. jarnoldae* were commonly used during “face-offs”, suggesting that they serve a similar function in this species. If these behaviours allow assessment of opponents during the establishment of dominance, we would have expected to see a decline in their use after the second day of the trial. However, the lizards continued to use colour-exposing behaviours equally both before and after a dominance relationship was apparent, suggesting that opponents still had reason to threaten each other.

Contest escalation also remained as high on the second day as on the first, with dominants continuing to pursue and harass subordinate lizards. This is surprising, since the dominance relationships evident on day 2 remained stable in all of the pairs we observed for up to 4 days (n=11), so reliable cues to the outcome of contests were clearly available. By continuing to display and engage in escalated interactions, individuals were likely to suffer in terms of time, energy, and potential injury.

The behaviour of *C. jarnoldae* contrasts with the findings of a behavioural study on another skink, the water skink *Eulamprus kosciuskoi* (Done & Heatwole, 1977). When small groups of water skinks were released into enclosures, fights and chases were initially frequent, but declined rapidly after the formation of a dominance hierarchy (Done & Heatwole, 1977). A possible reason for the differences in behaviour between *E. kosciuskoi* and *C. jarnoldae* is different social systems. The stable dominance hierarchies observed in captive *E. kosciuskoi* also appear to occur in the wild (Done & Heatwole, 1977). In contrast, *C. jarnoldae* is likely to be territorial in the wild (L. Schwarzkopf, unpublished data). Thus, continued aggression from dominant individuals to subordinates in this species may reflect the fact that territory owners are highly intolerant of intruders within their territories. Similarly, in male *Ctenotus fallens*, which are territorial in the wild, individuals that had been sole ‘residents’ in enclosures for 48 hours were extremely aggressive towards ‘intruders’ that were introduced into their territory (Jennings & Thompson, 1999). Thus, the

equally high levels of aggression and sustained use of throat presentations and raised postures by male *C. jarnoldae* after dominance relationships had emerged may indicate that the dominant individual was attempting to expel the subordinate from his territory. Although the lizards may have initially tried to settle conflicts through displays alone, the failure of the subordinate to leave the enclosure may have been interpreted by the dominant as failure to submit, and, therefore, contests inevitably escalated to violence.

Nevertheless, the behaviour of male *C. jarnoldae* was far less overtly aggressive than the fights and wrestling matches observed in some other lizards in captivity (e.g. *Ctenopus fallens*, Jennings & Thompson, 1999), suggesting that their displays are effective to some extent, even in captivity. It is likely that displays would be used with greater success in the field, where contests could be settled peacefully by early retreat of the loser (e.g., Maan et al., 2001).

Differences between Dominants & Subordinates

Display behaviours can be important not only during the acquisition of resources or status, but also in maintaining ownership of them. It benefits a dominant individual to be easily recognised so that subordinates can avoid contests with him (Rohwer, 1982). Subordinate individuals can benefit from recognising the dominant and subsequently avoiding trespassing on his territory or utilising other resources that he “owns” such as food or females, as such behaviour is likely to provoke aggression. Thus, dominant individuals perform more displays than subordinates in many species of lizards (e.g. *Eulamprus kosciuskoi*, *E. spehnomorphus*, Done & Heatwole, 1977; *Anolis sagrei*, Tokarz, 1985; *Anolis carolinensis*, Andrews & Summers, 1996; *Gallotia galloti galloti*, Molina-Borja et al., 1998).

In this study, we found that the behaviour of dominants and subordinates differed significantly in a number of ways. Dominants displayed more than subordinates did, head bobbing, head tilting, and tail waving (both distal third and full tail waves) at significantly higher rates, and spending a significantly greater amount of time head bobbing and tail waving. They also tended to use more elevated postures than subordinates, which exposed the bright orange colouration of their flanks. In contrast, subordinates behaved inconspicuously, adopting less elevated postures and rarely displaying. Thus, it appears that raised postures and displays in *C. jarnoldae* are indicative of dominance status. In addition to display behaviours, dominants also spent more time actively searching the enclosure for intruders by crawling and tongue flicking, and head turning, while subordinates tended to spend more time trying to escape.

Our finding that dominant individuals use head bobs and tail waves more than subordinates provides support for the view that these behaviours are broadcast signals of

territory ownership (Langkilde et al., in review). This is interesting, because tail waves were previously thought to be anti-predator behaviours, attracting predators' attention to the tail, which can be autotomised (Arnold, 1988; Pough et al., 2001). Head bob displays are commonly used by lizards to signal residency status (Carpenter & Ferguson, 1977; Fleishman, 1992), and are often performed by an individual as it moves around its activity range, even when no conspecifics are visible (Stamps, 1977).

Dominants also differed from subordinates in their use of substrates, spending more time on and around the shelter. Dominance status has been found to confer priority of access to important resources in other enclosure studies with lizards, such as food (Done & Heatwole, 1977), perch sites (Tokarz, 1985), access to mates (Done & Heatwole, 1977; Andrews & Summers, 1996), or occupation of superior areas within the enclosure (Fox et al., 1981). We found no difference between dominants and subordinates in the amount of space (number of sectors) used. It is likely that the enclosure was too small for the lizards to maintain exclusive areas, as home ranges in the field are approximately 15m² (L. Schwarzkopf, unpublished data). Nevertheless, defence of the shelter site was possible. This provided the most secure retreat site available within the enclosures, and also appeared to have been a favoured basking site.

Environmental Context of Behaviours

Although communication is often very beneficial to an individual's survival and reproduction, the effectiveness of signals is often constrained by environmental factors that control rates of transmission and attenuation. Therefore, selection favours signals that are emitted at the places, times and environmental conditions that maximise emission and transmission to the intended receivers (Endler, 1993). We found that dominant male *C. jarnoldae* did not display randomly with respect to substrate, light level, or location within the enclosure. Rather, they displayed most on the shelter (head bob and tail wave) and on the sand (tail wave), more in the full sun than either partial or full shade (head bob and tail wave), and more in the centre of the enclosure than at either end (head bob and tail wave). These preferences may have been used to enhance the efficiency with which the lizards' behavioural signals were transmitted through the environment.

The shelter represented a raised platform from which the lizard was probably more conspicuous to another lizard within the enclosure. However, the rocks also represented high points, and yet these were rarely used to display. It is possible that there was an interaction between substrate and location choice, since the shelter was in the centre of the enclosure, while the rocks were at either end.

While lizards head bobbed most on the shelter and rarely on the sand, they tail waved frequently on both the sand and shelter. This may reflect the different meanings attributed to each of these behaviours, or it may be a function of signal efficiency. Tail waves may be more conspicuous when performed at ground level than head bobs, which may be more conspicuous from a raised point. Iguanids typically use elevated perches to perform their territorial head bob displays (Stamps, 1977). However, the tendency to display more on the shelter may be due to the fact that this was often an item the lizards seemed to be fighting over, and by head bobbing on it, an individual may be signalling that he “owns” it, specifically, and not necessarily as a broadcast signal that he owns the whole territory, while tail waves might be more broad territorial ownership signals.

By choosing to display most in the sun, lizards may have been maximising the conspicuousness of their displays. During displays, the lizards often used raised postures (especially bask high), which expose the bright orange colouration of the flanks. Because sunlight contains abundant wavelengths in the orange part of the spectrum (Endler, 1990), direct sunlight probably enhanced the brightness of the lizards’ orange flanks. The importance of colour patches during male contests in jewel skinks is explored in another paper (Maclagan et al., MS).

Finally, by choosing to signal from the centre of the tank rather than at one end (even if that end is more familiar), dominant lizards may have increased the distance over which their display signals were effective. As mentioned earlier, the tendency to display most in the centre may be confounded with the fact that the centre contained the shelter. Another alternative is that lizards might have been displaying most in the centre of the tank because this was the boundary of their previously established territories. However, this seems unlikely, since both lizards frequently went out of their own side into their partner’s.

By increasing the efficiency of signal transmission, an individual might be able to defend a larger territory, or at least, spend less time patrolling and displaying from different points around the territory boundary. Active patrolling of territory borders in search of intruders is costly in time and energy, and reduces growth rate, probably because extensive travel requires energy and reduces the time available for foraging (Stamps & Eason, 1989). Furthermore, higher intrusion rates and overlap with neighbouring individuals can also reduce growth rates (Stamps & Eason, 1989).

Finally, it may not only be beneficial for an individual to transmit signals more effectively, but also to receive them. Use of the shelter may have been a means of gaining a vantage over the territory, allowing earlier detection of intruders. Early detection of intruders is important, because it may become harder to evict intruders after they have spent longer within the territory, and they may even take it over (Eason & Stamps, 1992). In addition,

undetected intruders are likely to utilise resources the owner is defending, such as food or mating opportunities (Eason & Stamps, 1992). Other territorial lizards typically chose elevated places as vantage and display posts within their territories (Stamps, 1977).

Conclusion

Male *C. jarnoldae* readily interacted with one another during paired trials, showing a range of aggressive and display behaviours. Head bobs and tail waves were used most when opponents first interacted, and may be important means of assessment during the establishment of dominance. However, the use of other displays such as raised postures and throat flashes involving the exposure of colour patches did not decrease over time, suggesting that individuals were still threatening each other. This is consistent with the fact that escalation did not decrease even after reliable cues to contest outcome were available, suggesting that males of this species will not tolerate intruders in their territory.

After dominance was established, dominants displayed significantly more than subordinates, supporting speculations that display behaviours in this species are used to signal territorial ownership.

Finally, the lizards chose to display in environmental contexts that maximised the conspicuousness of these signals, possibly a tactic that has evolved to enhance efficiency of territory defence.

The roles of body size and color during the establishment of dominance in male jewel skinks, *Carlia jarnoldae*

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ABSTRACT

Animals frequently use color patches as signals communicating fighting ability or territory holding capacity. Typically, scincid lizards are cryptically colored, and thought to have rudimentary social behavior not involving contests or territoriality. Male jewel skinks (*Carlia jarnoldae*), however, exhibit three bright color patches: green-blue throats, blue dorso-lateral spots, and orange flanks. We determined whether body size, the color (i.e., hue, value, chroma) of any of these patches, or the size of the orange flank patch were associated with dominance during paired male encounters. We also tested the prediction of “sequential assessment game” theory that contests should be more escalated when opponents are most similar in body size or color area. We found that body size was a very strong predictor of dominance in *C. jarnoldae*, but that the colors of the three patches were not. A trend for dominants to have larger orange patches relative to their body size than did subordinates approached significance, suggesting that color patch size may also influence the outcome of dominance relationships. Orange patch size may be more important in nature, acting as a long-distance visual cue to territory ownership and fighting ability, allowing individuals to avoid escalated conflicts by assessing each other from afar. Escalation increased rather than decreased with the difference between opponents in body mass, suggesting that dominant male jewel skinks will not tolerate intruders within their territory, and continue to escalate contests even with repeated intrusions by the same individual.

INTRODUCTION

Selection for male competitive ability may favor the evolution of conspicuous cues or “badges” of fighting ability, especially in populations with frequent interactions (Rohwer, 1982). Both contestants benefit from the use of such badges if costly fights with predictable outcomes can be avoided (Maynard Smith, 1974; Parker, 1974). Poor fighters can acquiesce without being injured or killed, while good fighters can save time and energy, and avoid risking injury themselves.

In addition, contests often involve certain sequences of displays in which opponents gain progressively more information about each other’s fighting ability (Parker 1974). Such

contests generally begin with the least costly displays, before progressing to more costly, but also more accurate, means of assessment. The more closely matched opponents are, the longer a contest should last and the further it should escalate, because it will take longer to assess who is the strongest (Enquist and Leimar, 1983; Payne, 1998). Thus, contests should only escalate to actual fighting when opponents are very closely matched (Stamps & Krishnan 1994; Molina-Borja et. al 1998; Earley et. al 2002; Olsson 1994). This is called the “sequential assessment game” (Enquist and Leimar, 1983).

Reptiles employ a variety of sexually dimorphic display structures and signals to advertise their competitive abilities to opponents (Carpenter and Ferguson, 1977; Cooper and Greenberg, 1992; Pough et al., 2001). A recent comparative study of display complexity in iguanid lizards suggests that intensity of male-male competition has been a significant factor in the evolution of complex signals in lizards (Ord et. al, 2001). In many lizards, males develop brightly colored patches on the body during the breeding season, the time when they frequently engage in contests, either directly over females, or over resources needed to attract females, such as territory (Cooper and Greenberg, 1992; Stamps, 1977). Many authors have suggested (Noble and Bradley, 1933), and several recent studies have shown (Olsson, 1994; Thompson and Moore, 1991) that male lizards use these badges to assess each other’s fighting ability (reviewed in Pough et al., 2001).

Nevertheless, no study has yet examined the use of color badges during male contests in skinks. This is probably because skinks are generally regarded as being cryptic, non-territorial, fossorial and secretive (Cooper and Greenberg, 1992; Stamps, 1977). However, we report in another paper (Maclagan et al., MS) that when paired and confined in enclosures, male jewel skinks, *Carlia jarnoldae*, behave aggressively, using a variety of behavioral displays to threaten and assess each other. Furthermore, males of this species are very colorful, possessing a series of blue spots within a black dorso-lateral band, and developing bright orange flanks and blue-green throats during the summer breeding season. Meanwhile, females are cryptic brown. Males appear to defend their home ranges from other males, and males with the largest territories are likely to overlap with the home ranges of more females (L. Schwarzkopf, unpublished data). Jewel skinks also have an extensive repertoire of display behaviors (Langkilde et al., in press), some of which appear to be involved in the establishment of dominance and signaling of territorial ownership (Maclagan et al., MS). Therefore, *C. jarnoldae* represents an excellent model species in which to investigate the role of coloration during male-male competition in skinks.

In this study, we examined whether body size, the color of the flank, throat or spots, or the size of the orange flank patch, are used as cues to fighting ability in male *C. jarnoldae*. We did this by staging male-male encounters in semi-natural outdoor enclosures and

determining which traits were associated with dominance. In addition, we tested the prediction of the sequential assessment game that contests should be more escalated and costly when opponents were most closely matched in body size, color, or size of the orange patch.

METHODS

Study Animals

Adult male *Carlia jarnoldae* were captured by hand from Campus Creek on the James Cook University campus (19°19'N, 146°45'E) in Townsville, Australia, between late January and early April 2003. Only healthy individuals with no outward signs of parasite infestation were used.

Individuals were weighed to the nearest 0.01g, and their snout-vent length (SVL) and tail length were measured to the nearest 0.05mm. The number and positions of any bite scars were noted. The hue, value and chroma of each of three color areas – flank (orange), dorso-lateral spots (blue) and throat (blue-green) - were scored using the Methuen Handbook of Color (Kornerup and Wanscher, 1963), either outdoors under full, unfiltered, natural sunlight, or indoors under two 100 watt halogen bulbs (which emit wavelengths covering 100% of the visual spectrum) mounted on the ceiling from opposing angles.

To measure the area of the orange flank patch, the right-hand-side of each individual was photographed using a Nikon Cool-Pix™ 990 digital camera. If a bite scar marred an individual's right-hand-side, his left-hand-side was photographed instead. Photographs were all taken under standardized conditions, in a specialized booth consisting of a white box (60 x 50 x 55cm), with a smaller white box (32 x 22 x 24cm) inside it. The smaller box served as a platform upon which the lizard was placed during photography, and had a ruler on its front surface to allow calibration of size of objects in the photograph. The camera was mounted on a tripod at a fixed distance (20cm) from the photography platform. The macro setting and the camera's built-in flash were used for all photos. The area of the orange patch was then estimated from the photos using the "magic wand" color selection tool in Adobe Photoshop 5.5 (Adobe Systems, Inc., 1999), in conjunction with the object area estimation function in UTHSCA Image Tool for Windows (Wilcox et al., 1996).

Paired Trials

We conducted paired trials in semi-natural outdoor enclosures in order to observe the establishment of dominance relationships. Individuals were assigned to pairs opportunistically. Partners were randomly marked with either one or two small dots of white correction pen (Pentel CO. LTD., Fine Point Correction Pen, Tokyo Japan) on top of the

head and snout, taking care to avoid the parietal eye. This allowed them to be easily identified from a distance, and did not appear to cause any changes in their behavior. A previous study of behavior in *C. jarnoldae* found that similar markings did not influence the lizards (Langkilde, 1999). Furthermore, because the dots were placed on top of the head, and most skink displays involving color are oriented laterally (Carpenter and Ferguson, 1977), it is unlikely that they influenced the lizards' perception of each other.

We were unable to catch enough lizards to use one per trial, so some lizards (n=14) were used in two trials. During their second trials, lizards were placed into a new enclosure with a new opponent for whom this was also a second trial. Dominance status of individuals in their first and second trials was not significantly related (Fisher's Exact Test, Fisher statistic=2.695, p=0.3257, n=14).

At the conclusion of each trial, individuals were examined for new bite wounds, re-weighed, and their colors re-scored. Eventually, all lizards were individually toe-clipped so that they could be excluded from future trials, and released at the site of capture.

Enclosures

Trials were conducted in four large (220 x 110 x 52cm) oval, semi-natural outdoor enclosures. Each enclosure could be divided into two equal halves by a removable partition consisting of a flexible plastic board painted grey to match the walls of the enclosure. Enclosures were situated within 1km of the site from which lizards were obtained, and received direct natural sunlight between approximately 0700 hrs and 1830 hrs each day. Each enclosure had a lid consisting of a light poly-tube frame supporting a combination of 50% and 80% shade cloth, which was propped up approximately 50cm on one side. This ensured that both full sun and a variety of shade densities were available within the enclosures. A strip of galvanized metal flashing surrounded the top rim of the enclosure and extended approximately 10cm inwards, preventing lizards from escaping. The substrate was sand with a sparse covering of leaf litter. Food was available in the form of invertebrates that entered the open tanks, and was supplemented approximately every three days by live mealworms (*Tenebrio molitor*) and crickets (*Acheta domestica*). Water was available *ad libitum* from a plastic tub (30 x 20 x 10cm) sunk into the substrate at each end of the enclosure. Each water tub contained at least one emergent rock, facilitating easy access to water and providing raised basking and display sites. In addition, each half of each enclosure was provided with a wooden shelter (35 x 26 x 4cm) adjacent to the removable partition. This provided a retreat site, and served as a raised platform for basking and displaying.

Each pair was randomly assigned to an enclosure, and one individual was randomly allocated to each side of the partition. Both individuals were placed into the enclosure at the

same time, at least 36 hours before the first observation took place. This period allowed individuals to recover from any stress caused by handling, to explore their surroundings, and to begin establishing a territory.

On the first day of the experiment, the partition was removed 35 minutes before the first observation. The two wooden shelters were also removed at this time, and a smaller wooden shelter (24 x 14cm) was placed into the centre of the enclosure. The lizards were then left to recover from the disturbance and to begin interacting with each other.

Behavioral Observations

Lizards were observed from behind a freestanding opaque blind at the western end of each enclosure. Blinds were never moved during the experimental period. Five minutes before the first observation began, the observer quietly moved into position behind the blind and began watching the lizards. This allowed lizards to habituate to the presence of the observer and continue with normal behavior.

Observations were made between 0730 hrs and 1100 hrs, the period when lizards are most active in the wild (Langkilde, 1999). A few exceptions occurred when morning observations were prevented by rain, and in these cases, observations were made as soon as possible after rain had ceased, but never after 1400 hrs.

Initially, pairs were observed for four days (n=11). However, as it became apparent that dominance relationships were almost always established and stable by the second day, observations were restricted to two days for subsequent trials.

Both lizards in a pair were observed for 15 minutes each per day, providing a total of 30 minutes of observation time per pair, per day. The second observation was made immediately after the first, and the order of observation was random. If a lizard was not visible (i.e., hiding under the shelter or under leaves) on his first observation attempt, the observer returned every 30 min until he had emerged.

Observations were made using a custom-written event-recording program on a Hewlett Packard 200LX palmtop computer. The program enabled the start and end time of all behaviors of the individual being observed (hereafter known as the 'focal' animal) to be recorded continuously, in units of seconds past midnight. By visually dividing the enclosure lengthwise and widthwise into nine sectors (3 x 3), the observer was also able to record the location of the focal animal. In addition, the behavior and location of the second individual (hereafter known as the 'stimulus' animal), and descriptions of any interactions that occurred were recorded using the program's note-taking function.

All areas of the enclosure were visible through the blind, except for the closest half of the 'near center' section, behind the water tub. If at any time the focal animal could not be

seen, and he was not known to be under the shelter, his behavior was recorded as “can’t see”. Where possible, if an individual was not visible for a portion of his observation period, the observation was continued until 15 minutes of visible behavior had been recorded.

Determination of Dominance

We defined dominance as the ability to win at points of conflict (Hand, 1986). Thus, we identified dominant and subordinate individuals by comparing the number of interactions they won and lost during the combined observation periods of each individual on each day. An ‘interaction’ was defined as any incident where one individual moved to within 50cm of his opponent in a deliberate manner, and ended when one lizard (the ‘loser’) moved away. An individual was considered ‘dominant’ if he won a majority of interactions, while his opponent was considered ‘subordinate’. If both individuals won an equal number of interactions, and at least two interactions were observed, they were considered ‘equal’. If fewer than two interactions were observed, the relationship was classed as ‘unknown’, since it was impossible to determine the relationship between the lizards.

Because most pairs had established a stable dominant-subordinate relationship by day 2, the dominance score calculated for day 2 was used as the final dominance score for each individual, except when observations could not be made on day 2, and the dominance score from day 1 was used.

Statistical Analysis of Traits

Only pairs in which a clear dominant-subordinate relationship could be determined by day 2 were included in statistical analyses of traits ($n=20$).

Overall differences between dominant and subordinate individuals in size traits (mass, SVL, tail length, size of orange patch), hue (of flank, throat and spots) and chroma (of flank, throat and spots) were tested using a non-parametric multivariate paired differences test (“Multi-Response Permutation Procedure for Blocked Data”, BLOSSOM version W2003.2). When the multivariate tests indicated that dominant and subordinate individuals differed for a group of variables, we determined which individual variables differed using Wilcoxon’s Signed Ranks tests. We performed these comparisons at comparisonwise significance levels of $\alpha=0.05$, since the initial multivariate tests ensured an experimentwise Type I error rate of $\alpha=0.05$. Because color value only varied in one color patch (spots), this was tested using a single Wilcoxon’s Signed Ranks test.

To determine whether the size of the orange patch differed between dominant and subordinate individuals, we conducted an analysis of covariance (ANCOVA) relating log-transformed values of area of the orange patch to body mass and dominance status.

Contest Escalation

In order to establish whether contests escalated more when opponents were most similar in body size or color traits, four estimates of ‘escalation’ were generated. For each pair per day we calculated: (i) the average number of interactions per minute, (ii) the average number of ‘intense’ interactions per minute (defined as interactions during which opponents were less than 20cm apart, or which ended in a chase), and (iii) the maximum ‘escalation’ level that was observed. ‘Escalation’ could take a value of 0 (meaning there was no interaction between opponents whatsoever), 1 (opponents displayed to each other, but did not interact directly), 2 (opponents had at least one interaction), or 3 (opponents had at least one intense interaction). The final escalation measure was (iv) the sum of the number of bites received by both individuals in a pair over the course of the trial.

Correlation analyses were conducted between each of the four escalation measures and the standardised differences between opponents in all body size and color traits (calculated as the absolute value of the difference between opponents, divided by the mean value of the two individuals).

RESULTS

Twenty-three trials were conducted using 48 lizards. Twenty of the 23 pairs exhibited a clear dominant-subordinate relationship by day 2.

Size Traits

Dominant and subordinate lizards differed significantly in size traits (MRBP, standardised test statistic $\delta = -7.083$, $p < 0.001$, $n = 17$). Dominant individuals were significantly heavier (Wilcoxon’s Signed Ranks test, $Z = -3.594$, $p < 0.001$, $n = 20$; Fig. 1a), larger in SVL ($Z = -3.316$, $p = 0.001$, $n = 20$; Fig. 1b), and had larger orange patches ($Z = -2.485$, $p = 0.013$, $n = 17$; Fig. 1c) but did not differ from subordinates in tail length ($Z = .952$, $p = .341$, $n = 20$).

The area of the orange patch was significantly correlated with body mass ($R^2 = 0.582$, $p < 0.001$, $n = 42$; Fig. 2). The ANCOVA analysis showed that there was a strong relationship between log area and log mass ($F_{1,33} = 33.695$, $p < 0.001$), and suggested that this relationship depended on dominance status (intercept: $F_{1,33} = 3.459$, $p = 0.072$; slope: $F_{1,33} = 3.737$, $p = 0.062$). Because this result is not significant, we cannot conclude that the relationship might not disappear in a larger sample of pairs, however in the pairs we examined, it is clear that the size of the orange patch increased with mass at different rates in dominant and subordinate individuals. Separate regression analyses for dominants (regression equation: $\log_{10}(\text{area of patch}) = 4.101 + 1.487(\log_{10}(\text{mass}))$; $r^2 = 0.564$, $p < 0.001$) and subordinates (regression equation: $\log_{10}(\text{area of patch}) = 4.575 + 0.744(\log_{10}(\text{mass}))$; $r^2 = 0.406$, $p < 0.004$), indicated

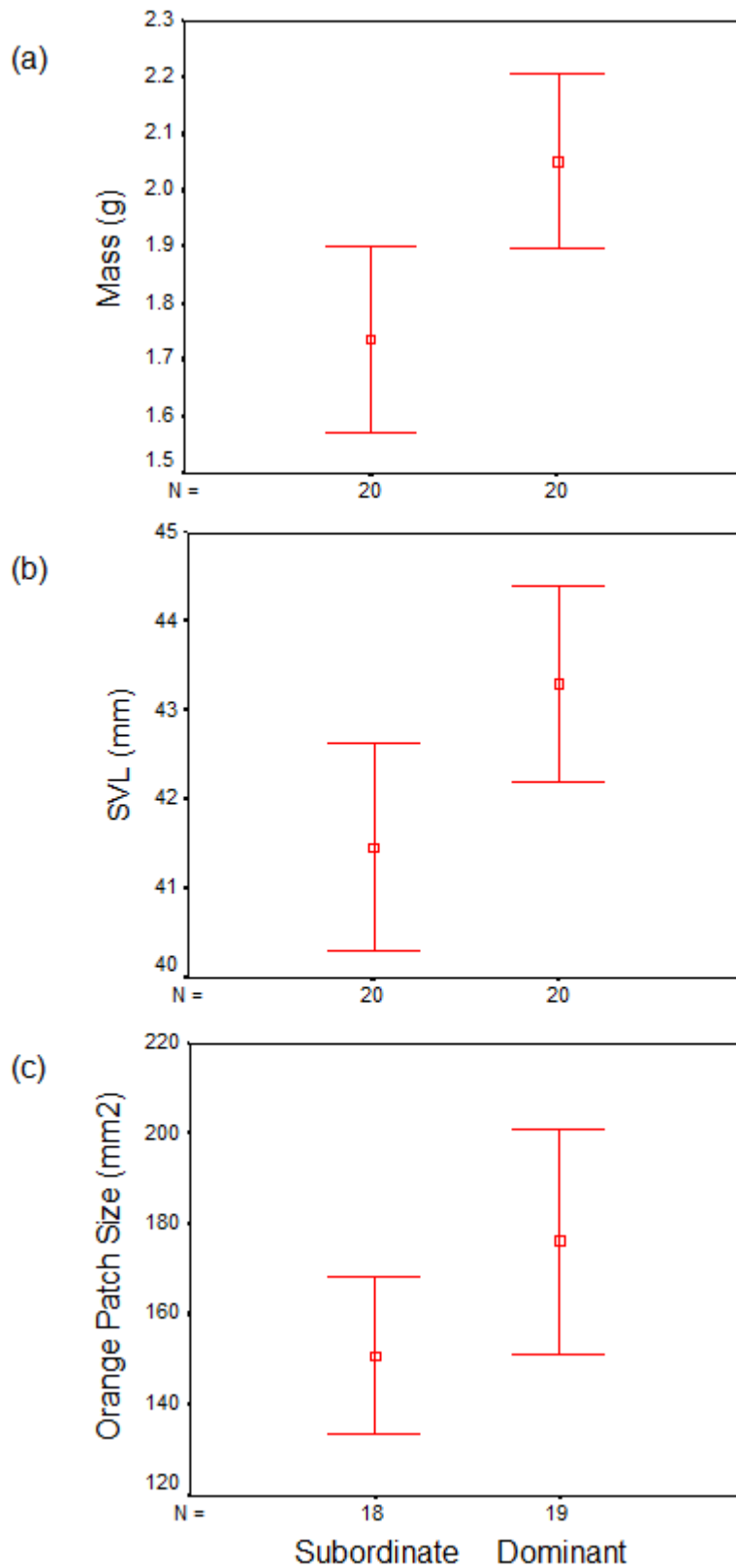


Fig. 1: Mean (\pm 95% CI) (a) mass, (b) snout-vent-length, and (c) orange patch size for dominant and subordinate lizards.

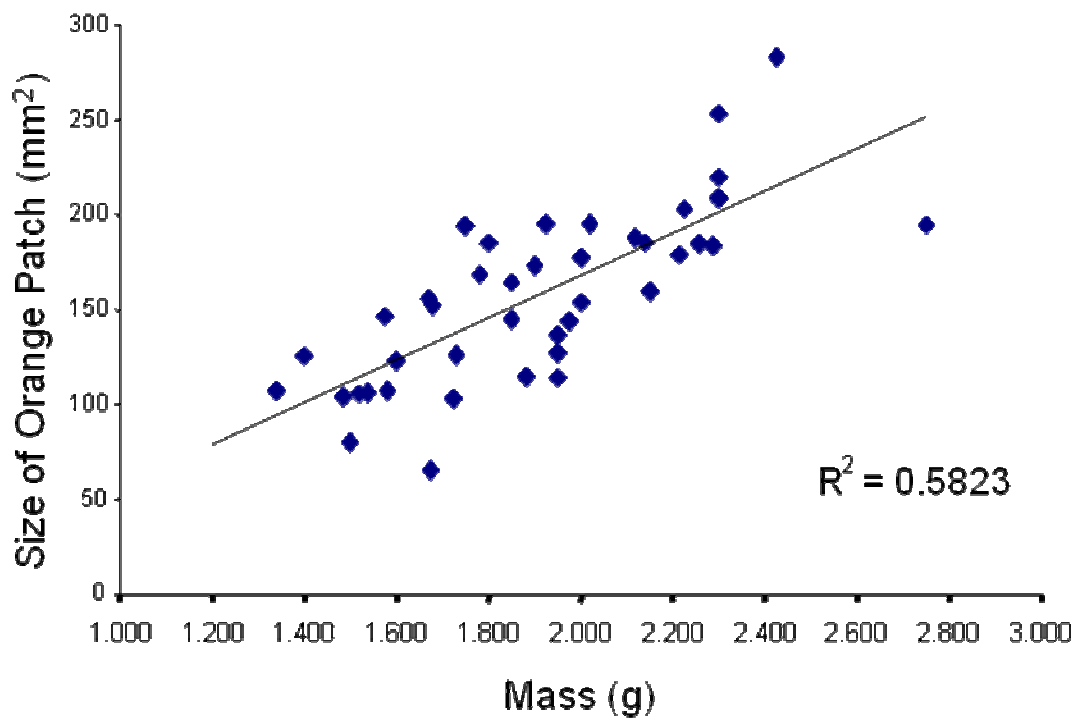


Fig. 2: Relationship between mass and size of orange patch in male *C. jarnoldae*.

that the size of the orange patch increased more rapidly with body size in dominants than subordinates. This implies that dominants tended to have larger orange patches relative to their body size than subordinates did.

Only in one pair did a slightly smaller male dominate a larger male, and this small male had a particularly large orange patch. In addition, in two pairs where lizards were identical in mass, the individual with the larger orange patch was dominant.

Color Traits

There were no overall differences between dominant and subordinate lizards in either the hues (MRBP, standardised test statistic $\delta=-0.088$, $p=0.37$, $n=20$) or chromas (MRBP, standardised test statistic $\delta=-0.032$, $p=0.423$, $n=20$) of the three color patches. Furthermore, the flank and throat values were identical for all individuals, and there was no significant difference in spot value between dominants and subordinates ($Z=-1.461$, $p=0.144$, $n=20$). Slight variation in color occurred within the same individual between repeat measurements, which were often conducted only a few days apart. Individuals tended to become gradually duller in color, until they moulted, and were once again brightly colored.

Contest Escalation

There were positive correlations between the standardized difference between opponents in mass, and both the maximum escalation on day 1 (Pearson correlation= $.501$, $r^2=0.2512$, $p_{\text{two-tailed}}=0.024$, $n=20$; Fig. 3) and the number of bites sustained over the trial (Pearson correlation= $.483$, $r^2=0.2446$, $p_{\text{two-tailed}}=0.019$, $n=23$; Fig. 4). This is the opposite of the relationship predicted by the sequential assessment game. Note that the second relationship is due to the presence of an outlier, and disappears if this point is removed. The outlying point represents a pair of lizards that were very disparate in size, in which the larger individual bit his small opponent repeatedly, eventually killing him before the second day of the trial. Consequently, we did not pair such disparately sized lizards again.

There were no other significant correlations between any of the four measures of escalation and the difference between partners in any of the other body size or color traits.

DISCUSSION

Body Size

Body size is a very strong predictor of dominance in male *C. jarnoldae* when opponents are symmetrical with respect to prior residency. This result is not surprising, since body size has been found to be an important predictor of dominance in many other lizards

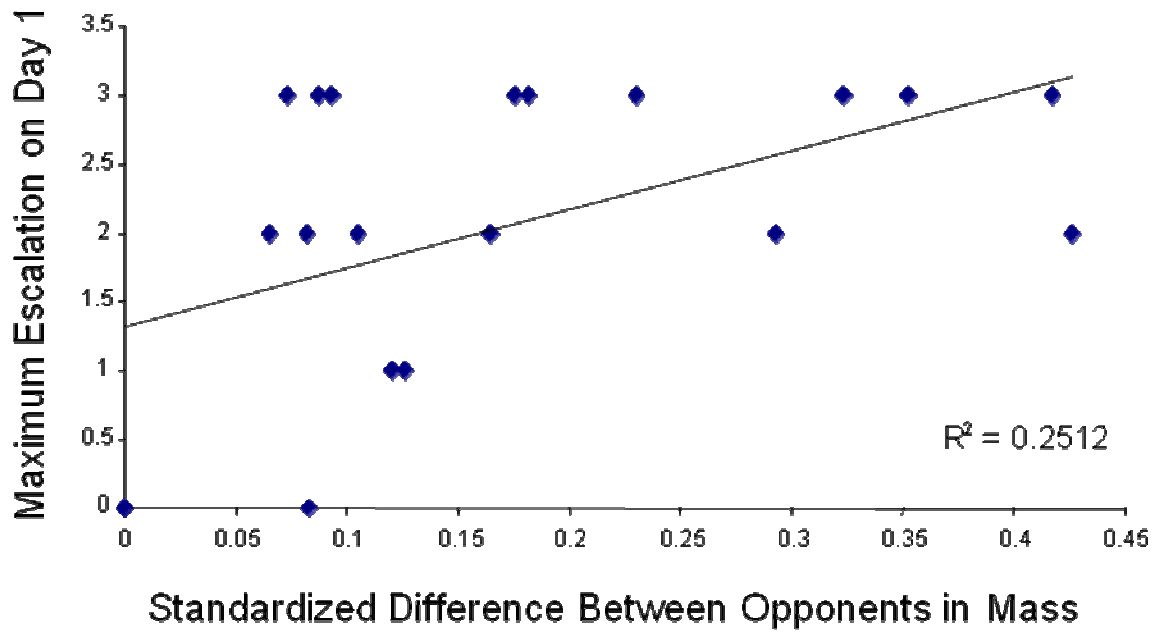


Fig. 3: Relationship between the standardized difference between opponents in mass (calculated as the absolute value of the difference between opponents in mass, divided by the average mass of the two individuals) and the maximum level of escalation observed on day 1.

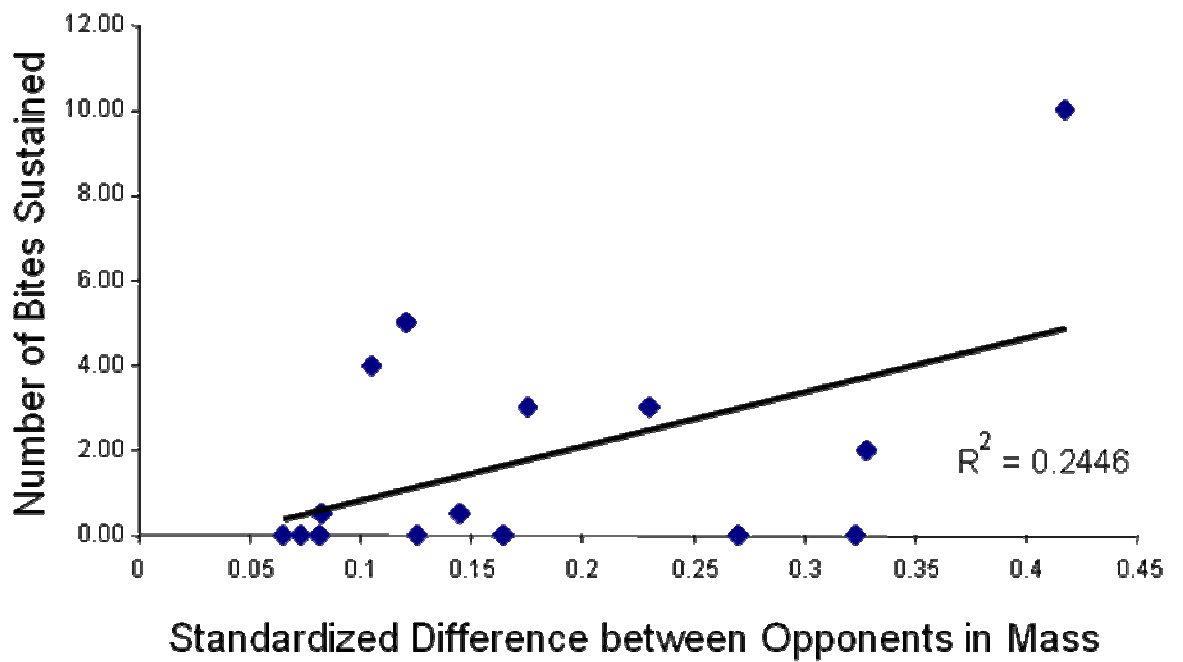


Fig. 4: Relationship between the standardised difference between opponents in mass (calculated as the absolute value of the difference between opponents in mass, divided by the average mass of the two individuals) and the total number of bite marks sustained by members of a pair over the course of the trial.

(reviewed in Pough et al., 2001), including the skinks *Eulamprus kosciuskoi*, *E. quoyi* (Done and Heatwole, 1977), *Eumeces laticeps*, (Cooper and Vitt, 1987), *Carlia rostralis* (Whittier and Martin, 1992) and *Lampropholis guichenoti* (Torr and Shine, 1996).

There are many possible reasons why large body size might confer greater fighting ability. Firstly, as male lizards generally fight by biting one another (Pough et al., 2001), larger individuals with bigger heads and more powerful jaws should be capable of inflicting greater damage (Bull and Pamula, 1996; Cooper and Vitt, 1987; Hews, 1990). Body size may also be correlated with age (and therefore fighting experience), general health and vigour, strength, and endurance, which are all likely to be important during fights (Andersson, 1994).

Orange Patch Size

Because the size of the lateral orange patch in male *C. jarnoldae* is correlated with body size, it may serve as a visual cue facilitating easier assessment of body size. In addition, it may function as an honest cue to individual vigour, since orange coloration in animals is usually carotenoid-based (Lozano, 1994; Olson and Owens, 1998). Vertebrates cannot synthesise carotenoids within their body, but must obtain them from the diet (Lozano, 1994; Olson and Owens, 1998). Therefore, both the extent and intensity of carotenoid pigmentation may reflect the ability of an individual to obtain, physiologically transport, process and deposit carotenoid pigments, tasks which are likely to depend on aspects of individual vigour, such as nutritional condition, parasite resistance, and immunocompetence (McGraw and Hill, 2000; Olson and Owens, 1998; Pryke et al., 2002; Pryke et al., 2001). The signalling properties of carotenoid pigmentation have been well established in birds. For example, in male red-collared widowbirds (*Euplectes ardens*) the saturation and extent of carotenoid-based plumage reflects individual fighting ability, and opponents use this to assess each other during male-male contests over territory (Pryke et al., 2001).

Consequently, males with bigger and brighter color patches defend bigger territories, spend less time in territory defence, and yet receive fewer intruders (Pryke et al., 2001).

Finally, orange coloration in lizards is often associated with high levels of aggression (*Eumeces fasciatus*, *E. inexpectatus*, *E. laticeps*, (Cooper and Vitt, 1988); *Carlia rostralis*, Whittier and Martin 1992; *Psammodromus algirus*, (Martin and Forsman, 1999); *Uta stansburiana*, (Sinervo et al., 2000). For example, male skinks of the genus *Eumeces* develop bright orange heads during the breeding season, which is the only time they exhibit aggressive behavior. The orange coloration is induced by androgens, which also activate sexual and aggressive behavior in this genus (Cooper and Vitt, 1988). Androgens are also

likely to be responsible for stimulating seasonal coloration in other lizards (Cooper and Greenberg, 1992).

Body size, vigour and aggression are all likely to be important determinants of fighting ability, so the lateral orange patch in *C. jarnoldae* may function as a visual cue to fighting ability. We found that body size and size of orange patch were both significantly larger in dominant than subordinate lizards, however, these traits were also correlated with each other, so it is difficult to say whether the orange patch would have influenced dominance on its own. However, in the pairs we examined, there was a non-significant trend for the size of the orange patch to increase more rapidly with body size in dominants than in subordinates, implying that dominants had larger orange patches relative to their body size. Thus, patch size may become an important predictor of dominance when differences between opponents in body size are small.

Studies on other lizards have successfully separated the effects of badge size from body size using manipulation experiments. For example, Olsson (1994) found that male sand lizards that had the extent of their lateral green color patches enlarged with green paint dominated individuals of the same size that had their green areas reduced to one third of their original size with brown paint. Similarly, Thompson and Moore (1991) found that male tree lizards, *Urosaurus ornatus*, use the color of the dewlap (extensible throat fan) to assess each other's fighting ability. Adult males have polychromatic dewlaps, which are either blue, yellow, orange, or bicolor combinations of an orange or yellow perimeter around a central blue spot that varies in size (Thompson and Moore, 1991). When the size of the central blue spot was manipulated, males with larger blue spots consistently won against males with smaller blue spots or dewlaps painted orange (Thompson and Moore, 1991). This pattern has also been observed between individuals with natural differences in dewlap color (Carpenter, 1995). Manipulation experiments could reveal whether the size of the orange patch is used as a signal of fighting ability in male *C. jarnoldae*.

Color

Hue, chroma, and value of the three colored patches (flank, throat and spots) did not differ between dominant and subordinate lizards in this study, suggesting that color is not an important determinant of dominance in male *C. jarnoldae*. Instead, it is likely that in this species, variation in hue, chroma and value is due to moulting stage, rather than to variation in fighting ability (or any other measure of fitness).

Bright coloration in *C. jarnoldae* may simply function as a cue to sex, allowing sex recognition from a distance, as has been found in many other lizard species (Cooper and Greenberg, 1992). Such cues may act as triggers for aggressive behavior in conspecific

males and of courting behavior in females (Carpenter and Ferguson, 1977). Furthermore, in species where both males and females partake in intra-sexual aggression, distinctive male coloration may exempt males from aggressive behavior from females. To investigate this possibility in *C. jarnoldae*, females could be painted to resemble males, and the responses of males observed.

In addition, color may be used to communicate territorial ownership. Even though color itself does not vary between individuals, dominant individuals may appear brighter by using behaviors that expose their coloration. For example, many male *Anolis* lizards incorporate extensions of their colorful dewlap into their territorial displays (Cooper and Greenberg, 1992). In *C. jarnoldae*, dominant individuals are significantly more likely to engage in behaviors that expose their colored patches, such as raised postures (basking high, body lifting) and throat presentation (throat flashes and head tilts; Maclagan et al., MS). Meanwhile, subordinates are more likely to adopt a flattened posture (bask flat) that conceals their coloration (Maclagan et al., MS). Thus, in *C. jarnoldae*, exposure of coloration by territory owners may allow intruders to recognise from a distance that an individual is male and a territory owner, and in this way steer clear of occupied territories and avoid costly fights.

Contest Escalation

In this study, the prediction that interactions should be more escalated and costly when opponents were similar in size or color was not supported. In fact, escalation measured as both the maximum escalation observed on day 1, and the number of bites received over the trial, were positively correlated with difference between partners in mass.

These results contrast with the predictions of the sequential assessment game (Enquist and Leimar, 1983), and the results of other studies in lizards, in which greater similarities between opponents in body size (Earley et al., 2002; Molina-Borja et al., 1998; Stamps and Krishnan, 1994) and badge size (Olsson, 1994) result in more escalated contests.

Nevertheless, results similar to ours have perplexed researchers during other experimental studies in lizards (reviewed in Stamps and Krishnan, 1998) and fish (Maan et al., 2001). Unnaturally high levels of escalation may result from certain artificial aspects of experimental situations (Maan et al. 2001). Firstly, staged encounters are often highly symmetrical, with opponents being matched for size, sex, territoriality and payoff. Such symmetric contests are probably rare in nature, where asymmetries such as ownership of territory can strongly influence chances of winning. However, in staged conflicts, both opponents may consider themselves territory owners trying to expel an intruder, resulting in long and escalated conflicts (Maan et al., 2001). The symmetry of the lizards with respect to

prior residency may therefore have contributed to the high escalation levels we observed in this study.

Second, unlike interactions in the wild, losers in staged conflicts are unable to escape from their opponents. As with many studies of territory acquisition in lizards (Stamps and Krishnan, 1998), our experiments were conducted in enclosures that were smaller than the lizards' natural territories, leaving the loser nowhere to retreat. Thus, the dominant individual may have continued to act aggressively towards him because he failed to leave the territory, as would presumably occur in the field. The positive correlation between maximum escalation on day 1 and the difference between opponents in mass probably reflects the fact that dominant individuals were more likely to closely approach and chase opponents that were much smaller than themselves.

Because of the high levels of escalation we observed, the importance of the orange patch size as a signal of fighting ability may have been underestimated in our trials, while that of body size may have been overestimated. Even if the lizards initially used visual cues to assess each other, they inevitably escalated to chases, which although costly, are a more accurate way to assess fighting ability.

In order to avoid the above limitations in future studies, experiments could be conducted in much larger enclosures, providing enough space for the dominant individual to set up an ample territory, while still leaving adequate space for the subordinate individual to retreat. It would also be interesting to make one half of the enclosure more desirable (i.e. by providing more shelter sites or food), to determine whether subordinate individuals are forced to retreat into the less desirable habitat.

General Discussion

Effective territorial defence requires the territory owner to detect and expel intruders in a timely fashion (Eason and Stamps, 1992). The greater the number of intruders, or the harder it is to detect them, the more time the owner must spend actively patrolling his territory. However, patrolling is a costly activity, and field studies have found that individuals who travel greater distances suffer lower growth rates, probably because of increased energy demands and reduced amount of time available for foraging (Stamps and Eason, 1989).

The costs of territory defence may be substantially reduced if an owner can deter intruders simply by sending signals from within the territory to show that it is occupied and that he is willing to fight for it. Intruders should benefit from taking heed of such signals, since the owner of a territory or other resource usually wins conflicts over it. There are three main reasons why this might be the case (Krebs and Davies, 1993): (1) owners are often

better fighters, since better fighters tend to become owners in the first place; (2) the resource may have greater value to the owner (who knows all the best basking and feeding spots, for example), so he is willing to fight harder for it; or (3) the evolutionarily stable strategy may be to accept a conventional rule, such as “owner always wins”. Thus, colors and other signals may enable residents to defer intruders from afar, and consequently defend larger areas than they would be able to by active patrolling alone.

It appears likely that long-distance visual cues are important for territory defence in male *C. jarnoldae*. Firstly, coloration as exposed by certain behaviors may signal territory ownership. In this species, dominant individuals use elevated postures and behavioral displays to appear more conspicuous, while subordinates display significantly less and use lower postures that conceal their lateral coloration (Maclagan *et. al* MS). Thus, territory owners appear to advertise their status using conspicuous behaviors, while intruders or subordinates adopt less conspicuous postures in an attempt to evade detection.

Secondly, the orange patch may provide long-distance cues to fighting ability. In male *C. jarnoldae*, the size of the orange flank patch may function as a visual cue to body size, which is directly related to fighting ability. In addition, the size or intensity of the orange patch may indicate individual vigour or aggressiveness. Such a cue would allow individuals to assess each other from afar and avoid costly escalated conflicts.

Visibility is often a major constraint on the ability of a species to defend territories (Stamps, 1977; Eason and Stamps, 1992; Fleishman, 1992). In fact, poor visibility both of a fossorial habitat, and of cryptic intruders is the reason commonly used to explain why skinks lack territoriality (Stamps 1977). However, *C. jarnoldae* are not fossorial, but inhabit rocky habitats such as dry creek-beds and creek banks in dry sclerophyll forest and savannah woodlands (Cogger 2000). The open rocky habitat is probably very good for the transmission of visual signals such as displays of color patches, since a variety of raised display sites are available (rocks), and there is little vegetation to obscure view. Furthermore, the lateral orange patches of male *C. jarnoldae* are significantly different from the color of the rocky backgrounds the skinks normally select (Rose, 1998). The combination of open habitat and bright coloration may be the key that has enabled *C. jarnoldae* to defend territories while other skinks do not (Stamps, 1977).

In conclusion, during escalated interactions between male *C. jarnoldae*, body size is a very strong determinant of dominance. In the wild, individuals may use behaviors that expose coloration and the size of the orange patch as long-distance visual cues to territory ownership and fighting ability, allowing them to assess each other from afar, and avoid costly escalated conflicts. Manipulation experiments would be useful in revealing whether this is indeed the case.

Final Report:

The establishment of dominance in male jewel skinks, *Carlia jarnoldae*: the roles of displays, body size and colouration

1 INTRODUCTION

This study represents a detailed examination of behaviour during the establishment of dominance relationships in male jewel skinks (*Carlia jarnoldae*). Unusually amongst skinks, this species shows striking sexual colour dimorphism (Cooper and Greenberg, 1992). Females are cryptic brown, but males possess bright blue spots on a black dorso-lateral stripe, and develop bright orange flanks and blue-green throats during the summer breeding season. Jewel skinks are endemic to northeastern Queensland, occurring in rocky habitats within dry sclerophyll forest and tropical woodlands (Cogger, 2000). Although they forage actively amongst leaf litter (Cogger, 2000), they are most commonly found basking and displaying on rocks (Rose, 1998). Most skinks lack territoriality, a pattern that has been attributed to their ground-dwelling habit and limited ability to detect nearby conspecifics (Stamps, 1977). However, field mark-recapture data suggest that both male and female jewel skinks may be intra-sexually territorial, as males occupy home ranges exclusive of other males, females occupy home ranges exclusive of other females, and males and females overlap with each other (L. Schwarzkopf, unpublished data). Finally, although most skinks are secretive, non-social, and lack complex behavioural displays (Cooper and Greenberg, 1992; Stamps, 1977), recent work suggests that jewel skinks are highly social, with a wide repertoire of display behaviours that appear to be used to communicate with conspecifics (Langkilde, 1999; Langkilde et al., in press). The jewel skink therefore appears to be a highly unusual member of the family Scincidae, and presents an exciting opportunity to expand our understanding of the diversity of social behaviour within this understudied taxon.

I staged paired contests between male jewel skinks in order to observe their social behaviour during male-male contests, and to determine which physical traits are related to dominance in this species. I also conducted a pilot study in which I manipulated the size of the lizards' orange flank patch in order to determine if this is an important determinant of dominance independent of the effects of body size.

My specific aims were to:

1. Describe the social behaviour of male jewel skinks during paired contests.
2. Describe how the lizards' behaviour changes over time, from when they first encounter one another to after a stable dominance relationship has been established.

3. Determine how the behaviour of dominant and subordinate individuals differs, and whether dominants are active over a greater area, or receive priority of access to important resources such as shelter and basking sites.
4. Examine whether the lizards choose to display in particular environmental contexts, such as different substrates, levels of light and location, which might maximise the conspicuousness of their displays.
5. Examine whether certain physical traits - body size, colour (hue, value or chroma) of the flank, throat or spots, or the size of the orange flank patch - are associated with dominance in male jewel skinks, and whether any of these appear to function as cues to fighting ability.
6. Test the predictions of the “sequential assessment game” (Enquist and Leimar, 1983) that contests should be more escalated and costly when opponents are more closely matched in body size, colour, or size of the orange patch.

2 GENERAL METHODS

2.1 Collection Site

I caught healthy-looking adult male lizards by hand from Campus Creek on the James Cook University campus, Townsville, (19°19'N, 146°45'E), in a section approximately 1km long, between the School of Tropical Veterinary Sciences and the North Queensland Cyclone Testing Facility. This stretch of creek has been found in previous years to be good habitat for jewel skinks.

2.2 Measurements

I weighed individuals to the nearest 0.01g using an electronic balance, and measured their snout-vent-length (SVL) and tail to the nearest 0.05mm. At this time, I also noted the number and positions of any bite marks.

2.2.2 Colour

I quantified the colour of the lizards' three coloured areas (orange flanks, blue dorso-lateral spots and blue-green throat) by estimating their hue, value and chroma using the Methuen Handbook of Colour (Kornerup and Wanscher, 1963) and the Munsell Book of Colour (Munsell, USA, 2003). I initially used only the Methuen system, because I did not have access to a Munsell colour chart until halfway through the sample season. I used both systems for the remainder of the sample season in the hope that they would be easily translatable, and that I could convert my earlier Methuen measurements to Munsell values at

the end. Unfortunately this was not the case, and I had to use only the Methuen colour estimates in my final analysis.

The recommended light in which to take measurements with the Methuen system is outdoors under unfiltered, natural sunlight (Kornerup and Wanscher, 1963), so that is what I initially did. However, when the wet season arrived (early February), outdoor measurements were often impossible due to heavy cloud or rain, so I began measuring colour indoors under two 100 watt halogen bulbs mounted on the ceiling from opposing angles. These emit wavelengths covering 100% of the visual spectrum, and provide a good approximation of natural sunlight.

2.2.3 Orange Patch Size

In order to measure the area of the orange patch on the lizard's flank, I developed a standardised method of photographing individuals and estimating their patch size from the photographs. I took photos in a specialised booth consisting of a large white box (60 x 50 x 55cm), with a smaller white box (32 x 22 x 24cm) inside it. The smaller box served as a platform for the lizard, and had a ruler attached to its front surface to allow calibration of the size of objects in the photograph, and on which I wrote the lizard's identification number and the date for later reference using non-permanent marker. I took photos using a Nikon Cool-Pix™ 990 digital camera mounted on a tripod at a fixed distance (20cm) from the photography platform. Using the camera's self-timer function so that my hands were free, I immobilised the lizard by gently holding its pelvis and head to ensure the flank was not twisted. For all photos, I used the camera's built-in flash (to provide full-spectrum light) and the macro setting. I photographed each lizard's right-hand-side, except when a bite scar marred it, in which case I photographed his left-hand-side instead.

I estimated the size of the orange patch by determining the number of pixels it covered in the photograph, and then converting this to millimetres using the ruler for calibration. First, the 'magic wand' function in Adobe Photoshop 5.5 (Adobe Systems, 1999) with a tolerance setting of 110 was used to select the orange patch. This shape was then cut from the photo and pasted into a new image. Any extra parts that were selected but were not part of the orange flank patch (such as the lizard's hind leg, my fingers, etc.) were erased at this point. Because the forearm was often orange, I carefully included a patch representing the estimated size of the base of the arm, by removing the remainder of the arm with the 'eraser' tool. I also had to standardise for the fact that in some individuals, the dark patch representing the axilla was fully surrounded by orange, and was therefore contained within the final orange patch, while other individuals did not have a complete ring of orange around their axilla, meaning that this area was not contained within in the final orange shape.

Therefore, I decided to include the axilla of all individuals by using the paintbrush tool to carefully draw around its perimeter, creating a smooth edge.

I then imported the shapes to UTHSCA Image Tool for Windows (Wilcox et al., 1996) and used the ‘analyse objects’ function to determine the number of pixels they covered. To convert pixel area to millimetres, I used the ‘distance’ tool to measure the number of pixels per selected number of millimetres on the calibration ruler in the original photograph, using the maximum number of millimetres visible in a continuous sequence (usually around 25mm). For each photo, I took the distance measure three times, and used the average of these as the final measure.

Finally, I calculated the area in mm^2 (A_{mm^2}) of the total orange area on a lizard’s flanks using the following formula, where A_p is the area in pixels of the orange shape, L_p is the length in pixels of the section of the calibration ruler, and L_{mm} is the length in millimetres of the section of the calibration ruler:

$$A_{\text{mm}^2} = 2A_p(L_{\text{mm}}/L_p)^2$$

Note that the value was multiplied by two to estimate the total area of orange on both sides of the lizard.

At the conclusion of each trial, I examined individuals for new bite scars, and re-weighed them so that I could calculate their average mass during the trial. All lizards were then individually toe-clipped so that they could be excluded from future trials, and released at the site of capture.

2.3 Manipulation of Orange Patch Size

Because I found that body size and the area of the orange patch were strongly positively correlated, I conducted a pilot study to separate the influence of these factors by manipulating orange patch size with paint. The first step was to find a type of paint that would adhere to the skinks’ smooth scales, that would not wash off in water (since they frequently ran through the water tubs when chased by their opponent, or by me when I attempted to catch them), and that would not affect their health. I tested various types of paint, including non-toxic acrylic fabric paint (Folkart, Plaid Enterprises, Inc., USA), oil-based paint marker pen (Uni Paint Marker, Mitsubishi Pencil Co. Ltd., Japan), acrylic model paint (Tamiya Colour Inc., Japan), and enamel model paint (Tamiya Colour Inc., Japan). I painted both flanks of one lizard with each type of paint, then held these individuals within small enclosures in a controlled environment room to closely monitor their health for the next three days. None of the lizards showed any signs of ill-health. The enamel model paint was deemed to be the best choice for use in my experiments, since it was superior to the fabric paint and acrylic model paint in that it was waterproof, and it was easier to apply and

was available in more appropriate colours than the paint marker pen. However, I still had to ensure the paint was a good approximation of the skinks' natural colour from another skink's point of view. I therefore had some painted chips scanned with a spectrometer by Dr. Justin Marshall at the University of Queensland, and compared these scans to scans previously done on live skinks at James Cook University by Lainy Day. There were no significant deviations between the two.

Using "buff" paint (XF-57, Tamiya Colour Inc., Japan), I reduced the orange patches of the slightly larger male in each pair to approximately 25% of their original size. This male was designated "dull", while his partner, "bright" did not have the size of his orange patches altered. However, to control for the effect of painting, I painted the flanks of the bright individual with transparent paint (X-22, Tamiya Colour Inc., Japan). Trials with painted individuals were otherwise exactly the same as other trials in which lizards were not painted.

2.4 Behavioural Observations

I observed pairs of male jewel skinks interacting within semi-natural outdoor enclosures (for detailed description of enclosures, see Chapter 1 or 2). Because prior residency can influence dominance in lizards (Stamps and Krishnan, 1998), I needed opponents to be symmetrical with respect to prior residency so that I could determine what physical features determine dominance. Therefore, opponents were initially held for a minimum period of 36 hours on opposite sides of an opaque removable barrier that divided the enclosure into two equal halves. During this acclimation period, each individual was provided with a wooden shelter (20 x 30cm) positioned adjacent to the centre barrier. On the morning the trial began, I removed centre partition and allowed the lizards to interact for the first time. I also removed the two wooden shelters and placed a single small wooden shelter (15 x 20cm) in the centre, providing a resource for the lizards to fight over. Thirty-five minutes later, I began recording the behaviour of one lizard (the 'focal' individual) from behind a blind, using a custom-written event-recording program on a Hewlett Packard 200LX palmtop computer. While this program was running, the computer screen displayed a key relating each of the lizards' 46 possible behaviours (devised by Langkilde, 1999) to a button on the keyboard (or a combination of "shift" and one of the buttons). After a few practice observations, it was possible to record all but the least common behaviours without having to look down. The program recorded the start and end time of each behaviour of the focal animal in units of seconds past midnight, which allowed both the frequency and duration of each behaviour to be calculated later. In addition, substrate (sand, rock, on shelter, half on shelter, under shelter, half under shelter), location (one of nine equal-sized sectors into which the enclosure was visually divided), or light (full sun, partial shade, full

shade), could be recorded continuously as well. It was also possible to add comments on the behaviour of the second lizard (the 'stimulus' individual), and to describe any interactions that occurred between the lizards.

I observed both individuals in a pair for 15 minutes each per day, totalling 30 minutes observation time per pair per day. Observations were conducted during the morning (07:30 – 11:00), when the lizards are most active. I initially conducted trials for 4 (n=7), 5 (n=3), or 6 (n=1) days. However, I found that the dominance relationships observed on day 2 never changed on subsequent days, so for the remainder of trials (n=24), I restricted observations to 2 days.

2.5 Determining Dominance

I assigned each lizard a daily dominance score based on the number of interactions he won and lost each day. An 'interaction' was any incident where one individual moved to within 50cm of his opponent in a deliberate manner, and ended when one lizard (the 'loser') moved away. An individual was considered 'dominant' if he won a majority of interactions, while his opponent was considered 'subordinate'. If both individuals won an equal number of interactions, they were considered 'equal'. If fewer than two interactions were observed, the relationship was classed as 'unknown'.

Because most pairs had established stable dominant-subordinate relationships by day 2, the dominance score calculated for day 2 was used as the final dominance score for each individual, except when observations could not be made on day 2, when I used the dominance score from day 1 (n=3 pairs).

Chemo-Sensory Trials

After noticing that the lizards often scraped the sides of their heads on the shelter or substrate ('mouth scrape'), usually during bouts of tongue-flicking, I suspected that this was a form of scent-marking. In order to find out, I designed an experiment to test whether skinks varied their tongue-flicking rates when presented with cotton swabs containing five different stimuli: the side of the mouth, the cloaca, the dorsum (a control of the skink's body), distilled water (a control for something liquid) and perfume (a control for something odorous). I used 20 individuals, who housed in small enclosures (15cm x 35cm x 10cm) and held in a controlled temperature room.

My first attempt involved placing the skink into a large, clean plastic container, holding the cotton-bud in front of its snout, and recording the number of tongue-flicks performed within 60 seconds after the first tongue-flick. Unfortunately this method was unsuccessful, as lizards were very fearful of me, and completely ignored the cotton bud.

To resolve this problem, I devised a specialised wooden blind consisting of two wooden panels fixed upright approximately 1m apart, one with a small oval viewing hole, and the other with a mirror attached above it. I then placed the cotton-bud into the container with the skink, then retreated immediately behind the blind and looked through the hole in the first board at the mirror above the second to observe the skink's behaviour in the container below. This method also proved unsuccessful, as the skinks simply watched me in the mirror. As their natural predators are birds, it is likely that skinks are particularly good at detecting overhead movement using their parietal eye. Nevertheless, I found that when I remained completely out of view for around 30 sec after depositing the cotton bud, the skinks were less likely to notice me.

However, at this point I encountered yet another problem. The skinks often tongue-flicked when they were far away from the cotton bud, in a seemingly exploratory manner. Although they did occasionally tongue-flick the cotton-bud directly, I found it extremely difficult to draw a distinct line between exploratory tongue-flicking and direct tongue-flicking of the cotton-bud. The rate of exploratory tongue-flicking was highly variable between individuals, and was not related to the type of scent on the cotton swab (individuals tongue-flicked as much with the distilled water control as with a cloaca smear). At this point, I felt I had spent too much time on what was supposed to be a minor side-project, and I gave up.

2 ANALYSIS, RESULTS & DISCUSSION

I staged 35 trials (with 25 non-painted pairs and 10 painted pairs) using 52 lizards, recording 42 hours of behaviour over 165 observation sessions. Because I was unable to catch enough lizards to use one per trial, some lizards (n=18) were used in two trials. However, during second trials, I always placed lizards into a new enclosure with a new opponent for whom it was also a second trial. Dominance status of individuals in their first and second trials was not significantly related (Fisher's Exact Test, Fisher statistic=3.228, p=0.2321, n=16).

The data from painted trials was included in analysis of behaviour, but excluded from analysis of traits related to dominance. Two trials were excluded from all analyses because one member of each pair died shortly after the trial, possibly due to heavy parasite infestation (which only became apparent after he died).

3.1 Social Behaviour

Male jewel skinks readily interacted with each other during paired contests, frequently engaging in aggressive interactions, and using a range of display behaviours to signal to each other. Common displays were 'head bobs', 'tail waves', throat presentations ('throat flashes'

and ‘head tilts’), and raised and tilted basking postures (‘bask high’, ‘body lift’ and ‘lateral tilt’). Throat presentations revealed the lizards’ blue-green gular colouration, while raised and tilted postures exposed the bright orange colouration on the lizards’ flanks. A full ethogram for *C. jarnoldae* is available in the literature (Langkilde et al., in press), and in the Glossary.

Fighting (wrestling) was never observed, but the lizards did engage in close “face-offs”, which often ended with one individual lunging at the other and chasing him around the enclosure. Although bites were hard to see as they are very fast, they apparently occurred during lunges and chases, as 21.6% of individuals (9.1% of dominants and 30.4% of subordinates) exhibited fresh bite wounds at the end of the trials.

By the second day of trials, 26 pairs had established clear dominant-subordinate relationships, while five pairs appeared equal, and in the remaining two pairs the relationship could not be determined because the lizards did not interact during observations. Thus, the majority of pairs established dominant-subordinate relationships within 48 hours of contact. These relationships remained stable in all of the pairs I observed for more than two days.

3.2 Changes in Behaviour Over Time

In order to see how the lizards’ behaviour changed as dominance relationships emerged, I compared the behaviour of individuals on the first and second day of the trials (n=43). I also tested whether contest behaviour of pairs was more escalated on day 1 or 2 (n=25; see Chapter 1 for escalation measures).

Trends for lizards to spend more time head bobbing and tail waving on the first day approached significance (see Figure 1, Chapter 1), but their use of other displays, postures and movement behaviours did not change over time. In addition, escalation remained as high on the second day as the first.

The greater use of head bobs and tail waves on day 1 suggests that these may be especially important during initial assessment of opponents, perhaps to signal residency status. Behaviours that expose the lizards’ bright colouration seem likely to be threat displays (as in the closely-related *Carlia rostralis*; Whittier and Martin, 1992), so their failure to decrease over time indicates that the lizards were still threatening each other even after a stable dominance relationship had been established. This coincides with the sustained escalation level on day 2.

It is initially surprising that lizards continued to display and engage in escalated interactions after dominance was settled, as these are likely to be costly activities. However, this may indicate that dominant individuals are intolerant of other males in the near vicinity. Jewel skinks appear to be territorial in the wild (L. Schwarzkopf, unpubl. data), so in the

enclosures, the dominant individual may have considered the subordinate to be an intruder within his territory, and therefore continued to behave aggressively towards him. Thus, although the lizards may have initially used displays to try to settle contests without physical aggression, they inevitably escalated to this because of their confinement within the enclosure.

3.3 Behavioural Differences of Dominants and Subordinates

I compared the behaviour of dominant and subordinate lizards on day 2, when dominance relationships had been established. Only pairs that had established a clear dominant-subordinate relationship, and in which both partners had been observed on day 2 (n=19) were included in analyses. I compared the use of various different behaviours, as well as duration spent on different substrates and in each section of the enclosure (where the enclosure was divided into three equal-sized sections: 'own side', on which the lizard was initially held, 'centre', and 'partner's side', on which his partner was initially held). I also compared an index of activity range (the number of enclosure sectors visited) and an index of movement (number of sectors entered per minute).

I found that dominants and subordinates differed in many ways, both in their behaviour and in their use of substrates and enclosure sections (see Figures 2-7 in Chapter 1). However, dominants and subordinates did not differ in their activity range or movement.

Dominants displayed more than subordinates, head bobbing, head tilting, and tail waving (both distal third and full tail waves) at significantly higher rates, and spending a significantly greater amount of time head bobbing and tail waving. They also used more elevated postures, during which the bright orange colouration of their flanks was exposed. Meanwhile, subordinates used lower basking postures, and they rarely displayed. While dominants appeared to be enhancing their conspicuousness, subordinates seemed to be trying to remain inconspicuous.

Dominants and subordinates also differed in their use of general activity behaviours, with dominants 'head turning', 'tongue-flicking', 'crawling', and 'crawling & tongue-flicking' significantly more. Although both dominants and subordinates scraped their mouths on the substrate, possibly as a scent-marking behaviour, dominants tended to do so more frequently. These behaviours may reflect the increased alertness of dominants as they surveyed their territory for intruders. Meanwhile, subordinates tended to spend slightly more time patrolling the enclosure perimeter and hanging on the enclosure wall, presumably trying to escape. However, dominants and subordinates did not differ in the number of times they jumped up the enclosure wall.

Dominants and subordinates also differed in their use of movement behaviours that were directly involved in aggressive interactions, either by initiating (approach, chase) or terminating (run, dart, flee) them. Dominant lizards approached and chased significantly more than subordinates, who very rarely approached, and never chased their opponents. Conversely, subordinate lizards spent significantly more time running and fleeing, and also tended to spend more time darting. These results are not surprising, given that I used behaviour during interactions as the basis for determining dominance.

Dominants and subordinates also differed in the amount of time they spent on different substrates and in different sections of the enclosure. Dominants spent significantly more time half on, under, and half under the shelter, while subordinates spent significantly more time on the sand. Dominants also tended to spend more time on the shelter and on the rocks than subordinates, although these differences are not significant. Dominants therefore appeared to gain priority of access to the shelter. This provided the most secure retreat site available within the enclosures, and was probably an attractive basking site.

Finally, dominants and subordinates differed in their use of the three different sections of the enclosure. While subordinates spent approximately equal proportions of time in all sections, dominant individuals spent more time in the centre. This may reflect the fact that dominants spent more time on the shelter, or in the centre where they could display more effectively and survey the tank for intruders.

3.4 Environmental Contexts of Behaviours

Because signal production can be costly, selection favours signals that are emitted at the places, times and environmental conditions that maximise transmission to the intended receivers (Endler, 1993). In order to see if jewel skinks select environmental contexts to enhance the conspicuousness of their displays, I examined whether they displayed at different rates or for different amounts of time on different substrates, light levels or in different sections the enclosure.

I found that displays did not occur randomly with respect to any of the contexts. Rather, lizards displayed most on the shelter (head bobs and tail waves) and on the sand (tail waves), more in the full sun than in either partial or full shade (head bobs and tail waves), and more in the centre of the enclosure than at either end (head bobs and tail waves).

The preference of the lizards for displaying in certain contexts seems likely to have been used to enhance the efficiency with which their signals were transmitted through the environment. The shelter represented a raised platform from which the lizard's displays were probably more conspicuous to another lizard within the enclosure. Tail waves also occurred

frequently on the sand, possibly because they are more conspicuous from ground level than head bobs, and therefore do not rely so heavily on a raised displaying point.

By choosing to display most in the sun, lizards may have made themselves, or their orange colouration more conspicuous. During displays such as head bobs and tail waves, they often used raised postures, which expose their flanks. Because sunlight contains abundant wavelengths in the orange part of the spectrum (Endler, 1990), direct sunlight probably enhanced the brightness of the lizards' orange flanks.

Finally, by choosing to signal from the centre of the tank rather than at one end (even if that end is more familiar), lizards may have increased the distance over which their display signals were effective. However, the tendency to display most in the centre may be confounded by the fact that the centre contained the shelter.

In jewel skinks, the significance of increasing the efficiency of signal transmission may be that an individual could defend a larger territory, or at least, spend less time patrolling and displaying from different points around the territory boundary, which are costly activities (Eason and Stamps, 1992).

3.5 Traits Related to Dominance

In order to determine what physical traits are related to dominance in male jewel skinks when opponents are symmetrical with respect to prior residency, I compared the traits of dominant and subordinate individuals. I used only data from non-painted pairs in which a clear dominance relationship was evident by day 2 ($n=20$).

I found that dominant lizards were significantly heavier, larger in SVL, and had larger orange patches than subordinates (see Figure 1, Chapter 2), but dominants and subordinates did not differ in tail length. The size of the orange patch was positively correlated with body size (see Figure 2, Chapter 2), so in order to determine if the relationship between body mass and the size of the orange patch was similar in dominants and subordinates, I conducted an analysis of covariance. There was a trend for the size of the orange patch to increase more rapidly with body size in dominants than in subordinates ($p = 0.062$), implying that dominants tended to have larger orange patches relative to their body size.

There were no overall differences between dominants and subordinates in any of the colour measures (hue, value, or chroma) of any of the three colour patches (flank, spots and throat).

Thus, of all the physical traits I measured, body size was the strongest predictor of dominance in male jewel skinks. This is consistent with the results of many other studies in lizards (reviewed in Pough et al., 2001). Body size may confer higher fighting ability, since

male lizards generally fight by biting one another, and larger males have larger heads capable of inflicting greater damage. In addition, body size may be correlated with other factors that determine fighting ability, such as age (and therefore fighting experience), general health and vigour, strength, and endurance (Andersson, 1994).

However, my results suggest that the size of the orange patch may also be related to dominance, especially when opponents are similar in body size. Because the size of the orange patch is correlated with body size, it may serve as a long-distance visual cue to body size. It may also be a cue to individual vigour, since orange pigmentation is usually carotenoid-based, and carotenoids are usually an honest indication of aspects of individual vigour, such as nutritional condition, parasite resistance, and immunocompetence (Lozano, 1994; McGraw and Hill, 2000; Olson and Owens, 1998; Pryke et al., 2002). Finally, the orange patch may reflect an individual's level of aggression, as orange colouration is probably stimulated by androgens (Cooper and Greenberg, 1992), and is associated with aggression in a number of other lizards (Cooper and Vitt, 1988); (Whittier and Martin, 1992); (Martin and Forsman, 1999); (Sinervo et al., 2000).

Precise colour parameters of the three colour patches appear unrelated to dominance in jewel skinks, as variation in colour is probably due to moulting stage rather than to variation in fighting ability. Instead, the distinctive colouration in jewel skinks may be a long-distance visual cue to sex, as it is in a number of other lizards (reviewed in Cooper and Greenberg, 1992). Furthermore, because dominant individuals are more likely to engage in behaviours that expose their colouration, wild lizards may expose their colouration as a signal of territorial ownership directed at conspecifics in the vicinity.

3.6 Manipulation Experiment Results

Painted trials were conducted near the end of the breeding season (early April), and unfortunately, the lizards were less active and less aggressive towards each other than in earlier trials. Dominance relationships were only established in six trials, while partners appeared to be equal in another two trials, and in the remaining two trials the relationship could not be determined because the opponents did not interact. Furthermore, in two of the trials in which a dominance relationship was established, individuals varied slightly in mass over the course of the trials such that the brighter individual ended up being larger than the manipulated individual with the smaller colour patch size. In both of these trials, the now larger bright individual was dominant. However, due to ambiguity, no conclusions can be made from these two pairs. The results of the six trials in which the bright individual was smaller, and in which the relationship could be determined are shown in Table 1, below:

TABLE 1: Outcomes of six painted trials.

Outcome	Number of Trials
'small bright' dominant	1
opponents equal	2
'large dull' dominant	3

Even when the size of their orange patch was reduced, larger individuals still tended to win trials. However, it is interesting that in one trial the small bright individual won, and that in two trials the opponents were equal, since in the twenty non-painted trials in which a dominant-subordinate relationship was evident, a smaller individual dominated a larger individual in only one trial. Thus, if colour manipulation had no effect whatsoever, we would have expected that large individuals with small colour patch sizes would win in all of the six trials. However, large lizards with manipulated colour patches were clear winners in only half.

Although these results are inconclusive, they suggest that when mass differences between opponents are small, the size of the colour patch may become an important determinant of dominance. Although individuals with reduced colour patches are of course unaware how they appear, 'bright' individuals may challenge them more often, eventually winning because of their higher aggression levels. Further painted trials should be conducted in order to find out if this is truly the case.

3.7 Sequential Assessment

The more closely matched opponents are, the longer a contest should last and the further it should escalate, because it will take longer to assess who is the strongest (Enquist and Leimar, 1983; Payne, 1998). In order to establish whether contests between male jewel skinks are more escalated when opponents are most similar in body size or colour traits, I calculated four measures of escalation (see Chapter 2), and correlated these with differences between partners in all of the body size and colour traits.

There were weak positive correlations between the difference in mass of opponents, and two measures of escalation: maximum escalation on day 1, and the number of bites sustained over the trial (although this second relationship is dependent on a strong outlier: see Figure 4, Chapter 2). Thus, escalation was higher when opponents were more different in mass. This pattern is opposite to that predicted by the sequential assessment game (Enquist and Leimar, 1983), and contrasts with the results of other studies in lizards, in which greater similarities between opponents resulted in more escalated contests (Earley et al., 2002; Molina-Borja et al., 1998; Olsson, 1994; Stamps and Krishnan, 1994).

However, as mentioned earlier, the high levels of aggression I observed may have been caused by the dominant continuing to try to expel the subordinate from his territory. The fact that escalation was higher when the subordinate was much smaller than the dominant probably reflects the fact that it is less risky for a dominant to harass an opponent much smaller than himself. Thus, the ability of male jewel skinks to settle conflicts through visual assessment may have been underestimated in these trials.

4 SUMMARY & CONCLUSIONS

When confined in enclosures, male jewel skinks readily interact with each other and almost always form dominant-subordinate relationships within 48 hours of contact. Although they do not appear to actually fight (i.e., wrestle), they engage in close face-offs, lunges and chases, which sometimes involve biting. They also use a variety of display behaviours, some of which appear to be most important during the initial stages of opponent assessment (head bobs and tail waves), and all of which are used more frequently by dominants than subordinates. These displays tend to be given in environmental contexts that maximise their conspicuousness to other lizards, and may be important for territorial defence in the field.

When opponents were confined in enclosures, body size was the strongest predictor of dominance in male jewel skinks, with larger males almost always dominating smaller ones. Neither the hue, value nor chroma of the three colour patches (flank, throat, spots) was an important predictor of dominance, and these may play some other role such as sex recognition. The size of the orange flank patch may influence dominance when differences between opponents in body size are very small, but the results of the present study only suggest this; further research is needed.

It is possible that the ability of lizards to resolve conflicts through displays and assessment of orange patch size was underestimated in this study, because lizards inevitably escalated to face-offs and chases due to their confinement within the enclosure, and the intolerance of dominants towards intruders. Thus, future experiments should be conducted in larger enclosures to provide subordinate individuals with the option of retreating before escalated conflict.

4.3 Future Research

This study opens the way to many avenues for further study. Firstly, it provides the groundwork and methods for a manipulation experiment to determine whether the size of the orange flank patch in male *C. jarnoldae* is used as a cue to fighting ability during male contests. Such an experiment should be carefully designed to provide subordinate individuals the chance to retreat from their opponents before conflicts escalate to violence.

In addition, it would also be interesting to examine whether body size or orange patch size is correlated to territory size or quality of lizards in the wild.

In order to find out whether the orange patch is truly an honest signal of individual quality, the relationship between patch size and parasite burden could be examined. Furthermore, skeletochronology could be used to determine whether orange patch size is related to age.

Another interesting manipulation experiment would involve painting female *C. jarnoldae* to resemble males (i.e., paint their flanks orange), and observing the response of males towards them. If males behave aggressively towards them, the importance of colouration in sex-recognition would be confirmed.

Finally, the genus *Carlia* presents an excellent opportunity for comparative studies to test hypotheses about relationships between colouration and ecology. Species in this group form a continuum of male brightness, from those that lack bright colouration, to those with very bright colouration. This study highlights the importance of conspicuousness for territory defence, and suggests that the notable conspicuousness of male *C. jarnoldae* may be the key to their ability to defend territory while other skinks do not. A comparative study could be used to test whether the degree of conspicuousness is correlated to degree of territoriality in the genus *Carlia*.

LITERATURE CITED: LITERATURE REVIEW

- Alford RA. 1999. Ecology: Resource use, competition and predation. Pp. 240-278 in *Tadpoles: The Biology of Anuran Larvae*. RW McDairmid and R Altig (eds). University of Chicago Press, Chicago.
- Andrén C, Henrickson L, Olsson M and Nilson G. 1988. Effects of pH and aluminium on embryonic and early larval stages of Swedish brown frogs, *Rana arvalis*, *R. temporaria*, and *R. dalmantina*. *Holarctic Ecology* **11**: 127-135.
- Baur A and Baur B. 1997. Seasonal variation in size and nutrient content of eggs of the land snail *Arianta arbustorum*. *Invertebrate Reproduction & Development* **32(1)**: 55-62.
- Benton TG and Grant A. 1999. Optimal reproductive effort in stochastic, density-dependent environments. *Evolution* **53(3)**: 677-688.
- Boulton AJ and Brock MA. 1999. *Australian Freshwater Ecology: Processes and Management*. Gleaneagles Publishing, Glen Osmond, South Australia.
- Bull JJ. 1987. Evolution of phenotypic variance. *Evolution* **41(2)**: 303-315.
- Capinera JL. 1979. Qualitative variation in plants and insects: Effect of propagule size on ecological plasticity. *Am. Nat.* **114(3)**: 350-361.
- Clutton-Brock TH. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton, New Jersey.
- Cooper WS and Kaplan RH. 1982. Adaptive “coin-flipping”: a decision-theoretic examination of natural selection for random individual variation. *Journal of Theoretical Biology* **94**: 135-151.
- Crump ML. 1981. Variation in propagule size as a function of environmental uncertainty for tree frogs. *Am. Nat.* **117(5)**: 724-737.
- Crump ML. 1984. Intraclutch egg size variability in *Hyla crucifer* (Anura: Hylidae). *Copeia* **1984(2)**: 302-308.
- Derickson WK. 1976. Ecological and physiological aspects of reproductive strategies in two lizards. *Ecology* **57**: 445-458.
- Dziminski MA. 2000. Intraclutch variation in egg provisioning in tropical Australian frogs: Its consequences for larval ecology. Honours thesis, James Cook University, Townsville.
- Ferguson GW and Fox SF. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards *Uta stansburiana*: its causes and evolutionary significance. *Evolution* **38**: 342-349.

- Fontes EG, Pires CSS and Sujii ER. 1995. Mixed risk-spreading strategies and the population dynamics of a Brazilian pasture pest, *Deois flavopicta* (Homoptera: Cercophidae). *Journal of Economic Entomology* **88**: 1256-1262.
- Forbes LS. 1999. Within-clutch variation in propagule size: the double-fault model. *Oikos* **85(1)**: 146-150.
- Gadgil M and Bossert W. 1970. Life history consequences of natural selection. *Am. Nat.* **104**: 1-24.
- Gillespie JH. 1974. Natural selection for within-generation variance in offspring number. *Genetics* **76**: 601-606.
- Griffiths RA. 1997. Temporary ponds as amphibian habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems* **7**: 119-126.
- Groeters FR. 1994. The adaptive role of facultative embryonic diapause in the grasshopper *Caledia captiva* (Orthoptera: Acrididae) in southeastern Australia. *Ecography* **17**: 223-233.
- Harper JL, Lovell PH and Moore KG. 1970. The shapes and sizes of seeds. *Annual Review of Ecology and Systematics* **1**: 327-356.
- Hays GC, Adams CR and Speakman JR. 1993. Reproductive investment by Green Turtles nesting on Ascension-Island. *Canadian Journal of Zoology* **71(6)**: 1098-1103.
- Hautek ete NC, Piquot Y and Van Dijk H. 2001. Investment in survival and reproduction along a semelparity-iteroparity gradient in the *Beta* species complex. *Journal of Evolutionary Biology* **14**: 795-804.
- Herbert PN and Sealy SG. 1993. Egg-size variation in Yellow Warblers – Apportionment of parental investment and the brood-survival hypothesis. *Canadian Journal of Zoology* **71(5)**: 1008-1011.
- Hopper KR. 1999. Risk-spreading and bet-hedging in insect population biology. *Annual Review of Entomology* **44**: 535-560.
- Jonsson A and Ebenman B. 2001. Are certain life histories particularly prone to local extinction? *Journal of Theoretical Biology* **209**: 455-463.
- Kaitala V, Tesar D and Ranta E. 2002. Semelparity versus iteroparity and the number of age groups. *Evolutionary Ecology Research* **4(2)**: 169-179.
- Kaplan RH. 1992. Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis*. *Ecology* **73**: 280-288.
- Kaplan RH and Cooper WS. 1984. The evolution of developmental plasticity in reproductive

- characteristics: An application of the “adaptive coin-flipping” principle. *Am. Nat.* **123(3)**: 393-410.
- Kaplan RH and King EG. 1997. Egg size is a developmentally plastic trait: Evidence from long-term studies in the frog *Bombina orientalis*. *Herpetologica* **53(1)**: 149-165.
- Kim JY and Thorp RW. 2001. Maternal investment and size-number trade-off in a bee, *Megachile apicalis*, in seasonal environments. *Oecologia* **126(3)**: 451-456.
- Krebs JR and Davies NB. 1993. *An Introduction to Behavioural Ecology*, 3rd Edition. Blackwell Science, Carlton, Victoria.
- Lack D. 1947. The significance of clutch-size. *Ibis* **89**: 302-352.
- Lips KR. 2001. Reproductive trade-offs and bet-hedging in *Hyla calypsa*, a Neotropical treefrog. *Oecologia* **128**: 509-518.
- Luddecke H. 2002. Variation and trade-off in reproductive output of the Andean frog *Hyla labialis*. *Oecologia* **130**: 403-410.
- Mazzoldi C, Poltroneiri C and Rasotto MB. 2002. Egg size variability and mating system in the marbled goby *Pomatoschistus marmoratus* (Pisces: Gobiidae). *Marine Ecology – Progress Series* **233**: 231-239.
- McGinley MA, Temme DH and Geber MA. 1987. Parental investment in offspring in variable environments: Theoretical and empirical considerations. *Am. Nat.* **130(3)**: 370-398.
- Menu F, Roebuck J and Viala M. 2000. Bet-hedging diapause strategies in stochastic environments. *Am. Nat.* **155(6)**: 724-734.
- Menu F and Desouhant E. 2002. Bet-hedging for variability in life cycle duration: bigger and later-emerging chestnut weevils have increased probability of a prolonged diapause. *Oecologia* **132**: 167-174.
- O'Connor RJ. 1978. Brood reduction in birds: Selection for fratricide, infanticide and suicide? *Animal Behaviour* **26**: 79-96.
- Olsson M and Madsen T. 2001. Between-year variation in determinants of offspring survival in the Sand Lizard, *Lacerta agilis*. *Functional Ecology* **15(4)**: 443-450.
- Parichy DM and Kaplan RH. 1992. Maternal effects on offspring growth and development depend on environmental quality in the frog *Bombina orientalis*. *Oecologia* **91**: 579-586.
- Parichy DM and Kaplan RH. 1995. Maternal investment and developmental plasticity: Functional consequences for locomotor performance of hatchling frog larvae. *Functional Ecology* **9**: 606-611.
- Philippi T and Seger J. 1989. Hedging one's evolutionary bets, revisited. *Trends in Ecology and Evolution* **4(2)**: 41-44.

- Philippi T. 1993. Bet-hedging germination of desert annuals: Variation among populations and maternal effects in *Lepidium lasiocarpum*. *Am. Nat.* **142**: 488-507.
- Poulin R and Hamilton WJ. 2000. Egg size variation as a function of environmental variability in parasitic trematodes. *Canadian Journal of Zoology* **78(4)**: 564-569.
- Real LA and Ellner S. 1992. Life history evolution in stochastic environments: A graphical mean-variance approach. *Ecology* **73(4)**: 1227-1236.
- Roff DA. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York.
- Roosenburg WM and Dunham AE. 1997. Allocation of reproductive output: Egg- and clutch-size variation in the Diamondback Terrapin. *Copeia* **1997(2)**: 290-297.
- Salthe SN. 1969. Reproductive modes and the number and sizes of ova in the Urodeles. *American Midland Naturalist* **81(2)**: 467-490.
- Savage RM. 1952. Ecological, physiological, and anatomical observations on some species of anuran tadpoles. *Proceedings of the Zoological Society of London* **122**: 467-514.
- Schultz DL. 1989. The evolution of phenotypic variance with iteroparity. *Evolution* **43(2)**: 473-475.
- Seger J and Brockmann HJ. 1987. What is bet-hedging? *Oxford Surveys on Evolutionary Biology* **4**: 182-211.
- Simons AM and Johnston MO. 1997. Developmental instability as a bet-hedging strategy. *Oikos* **82(2)**: 401-406.
- Simons AM. 2002. The continuity of microevolution and macroevolution. *J. Evol. Biol.* **15**: 688-701.
- Slatkin M. 1974. Hedging one's evolutionary bets. *Nature* **250**: 704-705.
- Smith CC and Fretwell SD. 1974. The optimal balance between size and number of offspring. *Am. Nat.* **108**: 499-506
- Stearns SC. 1993. *The Evolution of Life Histories*. Oxford University Press, Melbourne.
- Steinwascher K. 1978. Interference and exploitation competition among tadpoles of *Rana utricularia*. *Ecology* **59**: 1039-1046.
- Tejedo M and Reques R. 1992. Effects of egg size and density on metamorphic traits in tadpoles of the natterjack toad (*Bufo calamita*). *Journal of Herpetology*. **26**: 146-152.
- Wilbur HM. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. *Am. Nat.* **111**: 43-68.

- Williams DD. 1997. Temporary ponds and their invertebrate communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* **7**: 105-117.
- Williamson I and Bull CM. 1989. Life history variation in a population of the frog *Ranidella signifera*:
Egg size and early development. *Copeia* **1989**: 349-356.
- Winkler DW and Wallin K. 1987. Offspring size and number: A life history model linking effort per offspring and total effort. *Am. Nat.* **129(5)**: 708-720.
- Wootton RJ. 1979. Energy costs of egg production and environmental determinants of fecundity in Teleost fishes. *Symposium of the Zoological Society of London* **44**: 133-159.
- Yoshimura J and Jansen VAA. 1996. Evolution and population dynamics in stochastic environments. *Researches in Population Ecology* **38(2)**: 165-182.

LITERATURE CITED: INTRODUCTION

- Andersson M, 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Bradbury JW, Vehrencamp SL, 1998. *Principles of Animal Communication*. Sunderland, MA, USA: Sinauer Associates, Inc.
- Butcher GS, Rohwer S, 1989. The evolution of conspicuous and distinctive coloration for communication in birds. *Current Ornithology* 6:51-108.
- Carpenter CC, Ferguson GW, 1977. Variation and evolution of stereotyped behaviour in reptiles. In: *Biology of the Reptilia Vol. 7* (Gans C, Tinkle DW, eds). London: Academic Press; 335-554.
- Catchpole CK, Slater PJB, 1995. *Bird Song: Biological themes and variations*. Cambridge: Cambridge University Press.
- Cogger HG, 2000. *Reptiles and Amphibians of Australia*, 6th ed. Sydney: Reed New Holland.
- Cooper WE, Greenberg N, 1992. Reptilian colouration and behaviour. In: *Biology of the Reptilia, Vol. 18 (Physiology E, Hormones, Brain and Behaviour)* (Gans C, Crews D, eds). Chicago: The University of Chicago Press; 298-422.
- Davies NB, Halliday TR, 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* 275:683-685.
- Done BS, Heatwole H, 1977. Social behaviour of some Australian skinks. *Copeia* 1977:419-430.
- Enquist M, Leimar O, 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology* 102:387-410.
- Evans MR, Hatchwell BJ, 1992. An experimental study of male adornment in the scarlet-tufted malachite sunbird: I. The role of pectoral tufts in territorial defence. *Behavioural Ecology and Sociobiology* 29:413-419.
- Fleishman LJ, 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *The American Naturalist* 139, Supplement:S36-S61.
- Gould JL, Gould CG, 1989. *Sexual Selection*. New York: Scientific American Library.
- Greer AE, 1989. *The biology and evolution of Australian lizards*. Chipping Norton, NSW: Surrey Beatty & Sons PTY LTD.
- Hand JL, 1986. Resolution of social conflicts: dominance, egalitarianism, spheres of dominance and game theory. *The Quarterly Review of Biology* 61:201-220.
- Jennings BW, Thompson GG, 1999. Territorial Behaviour in the Australian scincid lizard *Ctenotus fallens*. *Herpetologica* 55:352-361.

- Krebs JR, Davies NB, 1993. An Introduction to Behavioural Ecology, 3rd ed. Oxford: Blackwell Science.
- Langkilde T, Schwarzkopf L, Alford RA, in press. An ethogram for the rainbow skink, *Carlia jarnoldae*. Herp. Journal.
- Maynard Smith J, 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology* 47:209-221.
- McMann S, 2000. Effects of residence time on displays during territory establishment in a lizard. *Animal Behaviour* 59:513-522.
- Morton ES, 1975. Ecological sources of selection on avian sounds. *American Naturalist* 109:17-34.
- Noble GK, Bradley HT, 1933. The mating behaviour of lizards; its bearing on the theory of sexual selection. *Annual New York Academy of Science* 35:25-100.
- Nowicki S, Searcy WA, Hughes M, 1998. The territory defence function of song in song sparrows: a test with the speaker occupation design. *Behavior* 135:615-628.
- Olsson M, 1994. Nuptial colouration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. *Animal Behaviour* 48:607-613.
- Ord TJ, Blumstein DT, Evans CS, 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of London B* 268:737-744.
- Parker GA, 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology* 47:223-243.
- Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, D WK, 2001. *Herpetology*, 2 ed. Upper Saddle River, NJ: Prentice Hall.
- Rankin PR, 1973. Untitled observations on *Cryptoblepharus virgatus*. *Herpetofauna* 6:25.
- Rohwer S, 1982. The evolution of reliable and unreliable badges of fighting ability. *American Zoologist* 22:531-546.
- Stamps J, 1977. Social behaviour and spacing patterns in lizards. In: *Biology of the Reptilia Vol. 7* (Gans C, Tinkle DW, eds). London: Academic Press; 265-334.
- Stephenson G, 1977. Notes on *Tiliqua gerrardii* in captivity. *Herpetofauna* 9:4-5.
- Thompson CW, Moore MC, 1991. Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. *Animal Behaviour* 42:745-753.
- Torr GA, Shine R, 1996. Patterns of dominance in the small scincid lizard *Lampropholis guichenoti*. *Journal of Herpetology* 30:230-237.
- Whittier JM, Martin J, 1992. Aspects of social behaviour and dominance in male rainbow skinks, *Carlia rostralis*. *Australian Journal of Zoology* 40:73-79.

LITERATURE CITED: CHAPTER 1

- Andrews, T. J. & Summers, C. H. (1996). Aggression, and the acquisition and function of social dominance in female *Anolis carolinensis*. — *Behaviour* 133, 1265-1279.
- Arnold, E. N. (1988). Caudal autotomy as a defence. — In: *Biology of the Reptilia* Vol. 16 (R. B. Huey, ed). A. R. Liss, New York, p. 235-274.
- BLOSSOM version W2003.2 (2003). Fort Collins Science Center. US Geological Survey, Fort Collins.
- Bradbury, J. W. & Vehrencamp, S. L. (1998). *Principles of Animal Communication*. — Sinauer Associates, Inc., Sunderland, MA, USA.
- Carpenter, C. C. & Ferguson, G. W. (1977). Variation and evolution of stereotyped behaviour in reptiles. — In: *Biology of the Reptilia* Vol. 7 (C. Gans & D. W. Tinkle, eds). Academic Press, London, p. 335-554.
- Catchpole, C. K. & Slater, P. J. B. (1995). *Bird Song: Biological themes and variations*. — Cambridge University Press, Cambridge.
- Cooper, W. E. & Greenberg, N. (1992). Reptilian colouration and behaviour. — In: *Biology of the Reptilia*, Vol. 18 (Physiology E, Hormones, Brain and Behaviour) (C. Gans & D. Crews, eds). The University of Chicago Press, Chicago, p. 298-422.
- Done, B. S. & Heatwole, H. (1977). Social behaviour of some Australian skinks. — *Copeia* 1977, 419-430.
- Eason, P. K. & Stamps, J. (1992). The effect of visibility on territory size and shape. — *Behavioral Ecology* 3, 166-172.
- Endler, J. A. (1990). Light, behaviour, and conservation of forest-dwelling organisms. — *Copeia* 1990, 1165-1168.
- . (1992). Signals, signal conditions, and the direction of evolution. — *The American Naturalist* 139, Supplement, S129-S153.
- . (1993). Some general comments on the evolution and design of animal communication systems. — *Philosophical Transactions of the Royal Society of London B* 340, 215-225.
- Ezaki, Y. (1995). Establishment and maintenance of the breeding territory in the polygynous great reed warbler. — *Ecological Research* 10, 359-368.
- Fleishman, L. J. (1992). The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. — *The American Naturalist* 139, Supplement, S36-S61.

- Fox, S. F., Rose, E. & Myers, R. (1981). Dominance and the acquisition of superior home ranges in the lizard *Uta stansburiana*. — *Ecology* 62, 888-893.
- Gould, J. L. & Gould, C. G. (1989). *Sexual Selection*. — Scientific American Library, New York.
- Gwinner, E., Rodl, T. & Schwabl, H. (1994). Pair territoriality of wintering stonechats: behaviour, function and hormones. — *Behavioural Ecology and Sociobiology* 34, 321-327.
- Hand, J. L. (1986). Resolution of social conflicts: dominance, egalitarianism, spheres of dominance and game theory. — *The Quarterly Review of Biology* 61, 201-220.
- Jennings, B. W. & Thompson, G. G. (1999). Territorial Behaviour in the Australian scincid lizard *Ctenotus fallens*. — *Herpetologica* 55, 352-361.
- Langkilde, T. (1999). Tails as a signalling system in skinks: their function and the consequences of their loss. — Honours, James Cook University.
- Langkilde, T., Schwarzkopf, L., Alford, R.A. Minimising the predation risk associated with broadcast displays by signalling with an "expendable" body part (in review, *Animal Behaviour*)
- Langkilde, T., Schwarzkopf, L. & Alford, R. A. (in press). An ethogram for the rainbow skink, *Carlia jarnoldae*. — *Herp. Journal*.
- Maan, M. E., Groothuis, T. G. G. & Wittenberg, J. (2001). Escalated fighting despite predictors of conflict outcome: solving the paradox in a South American cichlid fish. — *Animal Behaviour* 62, 623-634.
- Maclagan, S., Schwarzkopf, L. & Alford, R. (MS). The roles of body size and colour during the establishment of dominance in male jewel skinks, *Carlia jarnoldae*. To be submitted to *Behavioral Ecology*.
- Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. — *Journal of Theoretical Biology* 47, 209-221.
- McMann, S. (2000). Effects of residence time on displays during territory establishment in a lizard. — *Animal Behaviour* 59, 513-522.
- Molina-Borja, M., Padron-Fumero, M. & Alfonso-Martin, T. (1998). Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (family Lacertidae). — *Ethology* 104, 314-322.
- Nowicki, S., Searcy, W. A. & Hughes, M. (1998). The territory defence function of song in song sparrows: a test with the speaker occupation design. — *Behavior* 135, 615-628.
- Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. — *Journal of Theoretical Biology* 47, 223-243.

- Pough, F. H., Andrews, R. M., Cadle, J. E., Crump, M. L., Savitzky, A. H. & D, W. K. (2001). Herpetology. — Prentice Hall, Upper Saddle River, NJ.
- Rohwer, S. (1982). The evolution of reliable and unreliable badges of fighting ability. — *American Zoologist* 22, 531-546.
- Stamps, J. (1977). Social behaviour and spacing patterns in lizards. — In: *Biology of the Reptilia* Vol. 7 (C. Gans & D. W. Tinkle, eds). Academic Press, London, p. 265-334.
- Stamps, J. & Eason, P. K. (1989). Relationships between spacing behavior and growth rates: a field study of lizard feeding territories. — *Behavioural Ecology and Sociobiology* 28, 29-36.
- Stamps, J. A. & Krishnan, V. V. (1997). Functions of fights in territory establishment. — *The American Naturalist* 150, 393-405.
- Tokarz, R. R. (1985). Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). — *Animal Behaviour* 1985, 746-753.
- van den Assem, J. & van der Molen, J. (1969). Waning of the aggressive response in the three-spined stickleback upon constant exposure to a conspecific. I. A preliminary analysis of the phenomenon. — *Behaviour* 34, 286-324.
- Whittier, J. M. & Martin, J. (1992). Aspects of social behaviour and dominance in male rainbow skinks, *Carlia rostralis*. — *Australian Journal of Zoology* 40, 73-79.
- Wickman, P. O. & Wiklund, C. (1983). Territorial defence and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). — *Animal Behaviour* 31, 1206-1216.

LITERATURE CITED: CHAPTER 2

- Adobe Systems, Inc., 1999. Adobe Photoshop 5.5. USA.
- Andersson M, 1994. Sexual Selection. Princeton, NJ: Princeton University Press.
- BLOSSOM version W2003.2, Fort Collins Science Center. US Geological Survey, Fort Collins.
- Bull CM, Pamula Y, 1996. Sexually dimorphic head sizes and reproductive success in the sleepy lizard *Tiliqua rugosa*. *Journal of Zoology* 240:511-521.
- Carpenter CC, 1995. Modeling dominance: the influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetological Monographs* 9:88-101.
- Carpenter CC, Ferguson GW, 1977. Variation and evolution of stereotyped behaviour in reptiles. In: *Biology of the Reptilia Vol. 7* (Gans C, Tinkle DW, eds). London: Academic Press; 335-554.
- Cooper WE, Greenberg N, 1992. Reptilian colouration and behaviour. In: *Biology of the Reptilia, Vol. 18 (Physiology E, Hormones, Brain and Behaviour)* (Gans C, Crews D, eds). Chicago: The University of Chicago Press; 298-422.
- Cooper WE, Vitt LJ, 1987. Deferred agonistic behavior in a long-lived scincid lizard *Eumeces laticeps*: field and laboratory data on the roles of body size and residence in agonistic strategy. *Oecologia* 72:321-326.
- Cooper WE, Vitt LJ, 1988. Orange head colouration of the male broad-headed skink (*Eumeces laticeps*), a sexually selected social cue. *Copeia* 1988:1-6.
- Done BS, Heatwole H, 1977. Social behaviour of some Australian skinks. *Copeia* 1977:419-430.
- Earley RL, Attum O, Eason PK, 2002. Varanid combat: perspectives from game theory. *Amphibia-Reptilia* 23:469-485.
- Eason PK, Stamps J, 1992. The effect of visibility on territory size and shape. *Behavioral Ecology* 3:166-172.
- Enquist M, Leimar O, 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology* 102:387-410.
- Hand JL, 1986. Resolution of social conflicts: dominance, egalitarianism, spheres of dominance and game theory. *The Quarterly Review of Biology* 61:201-220.
- Hews DK, 1990. Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. *Evolution* 44:1956-1966.
- Kornerup A, Wanscher JH, 1963. *Methuen Handbook of Colour*. London: Methuen & Co. LTD.

- Krebs JR, Davies NB, 1993. An Introduction to Behavioural Ecology, 3rd ed. Oxford: Blackwell Science.
- Langkilde T, 1999. Tails as a signalling system in skinks: their function and the consequences of their loss (Honours). Townsville: James Cook University.
- Langkilde T, Schwarzkopf L, Alford RA, in press. An ethogram for the rainbow skink, *Carlia jarnoldae*. Herp. Journal.
- Lozano GA, 1994. Carotenoids, parasites, and sexual selection. *Oikos* 70:309-311.
- Maan ME, Groothuis TGG, Wittenberg J, 2001. Escalated fighting despite predictors of conflict outcome: solving the paradox in a South American cichlid fish. *Animal Behaviour* 62:623-634.
- Maclagan S, Schwarzkopf L, Alford, R, MS. Display behaviors and the establishment of dominance in male jewel skinks, *Carlia jarnoldae*. *Behavior*.
- Martin J, Forsman A, 1999. Social costs and development of nuptial coloration in male *Psammadromus algirus* lizards: an experiment. *Behavioral Ecology* 10:396-400.
- Maynard Smith J, 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology* 47:209-221.
- McGraw KJ, Hill GE, 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London B* 267:1525-1531.
- Molina-Borja M, Padron-Fumero M, Alfonso-Martin T, 1998. Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (family Lacertidae). *Ethology* 104:314-322.
- Noble GK, Bradley HT, 1933. The mating behaviour of lizards; its bearing on the theory of sexual selection. *Annual New York Academy of Science* 35:25-100.
- Olson VA, Owens IPF, 1998. Costly sexual signals: Are carotenoids rare, risky or required? *Trends in Ecology and Evolution* 13:510-514.
- Olsson M, 1994. Nuptial colouration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. *Animal Behaviour* 48:607-613.
- Parker GA, 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology* 47:223-243.
- Payne RJH, 1998. Gradually escalating fights and displays: the cumulative assessment model. *Animal Behaviour* 56:651-662.
- Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, D WK, 2001. *Herpetology*, 2 ed. Upper Saddle River, NJ: Prentice Hall.

- Pryke SR, Andersson S, Lawes MJ, Piper SE, 2002. Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behavioral Ecology* 13:622-631.
- Pryke SR, Lawes MJ, Andersson S, 2001. Agonistic carotenoid signalling in male red-collared widowbirds: Aggression related to the colour signal of both the territory owner and model intruder. *Animal Behaviour* 62:695-704.
- Rohwer S, 1982. The evolution of reliable and unreliable badges of fighting ability. *American Zoologist* 22:531-546.
- Rose S, 1998. Background matching and thermal ecology in tropical scincid lizards (Honours). Townsville: James Cook University.
- Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF, 2000. Testosterone, endurance, and darwinian fitness: Natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior* 38:222-233.
- Stamps J, 1977. Social behaviour and spacing patterns in lizards. In: *Biology of the Reptilia Vol. 7* (Gans C, Tinkle DW, eds). London: Academic Press; 265-334.
- Stamps J, Eason PK, 1989. Relationships between spacing behavior and growth rates: a field study of lizard feeding territories. *Behavioural Ecology and Sociobiology* 28:29-36.
- Stamps JA, Krishnan VV, 1994. Territory acquisition in lizards: II. Establishing social and spatial relationships. *Animal Behaviour* 47:1387-1400.
- Stamps JA, Krishnan VV, 1998. Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. *Animal Behaviour* 55:461-472.
- Thompson CW, Moore MC, 1991. Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. *Animal Behaviour* 42:745-753.
- Torr GA, Shine R, 1996. Patterns of dominance in the small scincid lizard *Lampropholis guichenoti*. *Journal of Herpetology* 30:230-237.
- Whittier JM, Martin J, 1992. Aspects of social behaviour and dominance in male rainbow skinks, *Carlia rostralis*. *Australian Journal of Zoology* 40:73-79.
- Wilcox D, Dove B, McDavid D, Greer D, 1996. UTHSCA Image Tool for Windows. In, 2.00 ed. San Antonio, Texas: The University of Texas Health Science Centre in Antonio.

LITERATURE CITED: FINAL REPORT

- Adobe Systems I, 1999. Adobe Photoshop 5.5. In. USA.
- Andersson M, 1994. Sexual Selection. Princeton, NJ: Princeton University Press.
- Cogger HG, 2000. Reptiles and Amphibians of Australia, 6th ed. Sydney: Reed New Holland.
- Cooper WE, Greenberg N, 1992. Reptilian colouration and behaviour. In: Biology of the Reptilia, Vol. 18 (Physiology E, Hormones, Brain and Behaviour) (Gans C, Crews D, eds). Chicago: The University of Chicago Press; 298-422.
- Cooper WE, Vitt LJ, 1988. Orange head colouration of the male broad-headed skink (*Eumeces laticeps*), a sexually selected social cue. *Copeia* 1988:1-6.
- Earley RL, Attum O, Eason PK, 2002. Varanid combat: perspectives from game theory. *Amphibia-Reptilia* 23:469-485.
- Eason PK, Stamps J, 1992. The effect of visibility on territory size and shape. *Behavioral Ecology* 3:166-172.
- Endler JA, 1990. Light, behaviour, and conservation of forest-dwelling organisms. *Copeia* 1990:1165-1168.
- Endler JA, 1993. Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London B* 340:215-225.
- Enquist M, Leimar O, 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology* 102:387-410.
- Kornerup A, Wanscher JH, 1963. *Methuen Handbook of Colour*. London: Methuen & Co. LTD.
- Langkilde T, 1999. Tails as a signalling system in skinks: their function and the consequences of their loss (Honours). Townsville: James Cook University.
- Langkilde T, Schwarzkopf L, Alford RA, in press. An ethogram for the rainbow skink, *Carlia jarnoldae*. *Herp. Journal*.
- Lozano GA, 1994. Carotenoids, parasites, and sexual selection. *Oikos* 70:309-311.
- Munsell Color Services, 2003. *The Munsell Book of Color*. New Windsor, NY.
- Martin J, Forsman A, 1999. Social costs and development of nuptial coloration in male *Psammadromus algirus* lizards: an experiment. *Behavioral Ecology* 10:396-400.
- McGraw KJ, Hill GE, 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London B* 267:1525-1531.

- Molina-Borja M, Padron-Fumero M, Alfonso-Martin T, 1998. Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (family Lacertidae). *Ethology* 104:314-322.
- Olson VA, Owens IPF, 1998. Costly sexual signals: Are carotenoids rare, risky or required? *Trends in Ecology and Evolution* 13:510-514.
- Olsson M, 1994. Nuptial colouration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. *Animal Behaviour* 48:607-613.
- Payne RJH, 1998. Gradually escalating fights and displays: the cumulative assessment model. *Animal Behaviour* 56:651-662.
- Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, D WK, 2001. *Herpetology*, 2 ed. Upper Saddle River, NJ: Prentice Hall.
- Pryke SR, Andersson S, Lawes MJ, Piper SE, 2002. Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behavioral Ecology* 13:622-631.
- Rose S, 1998. Background matching and thermal ecology in tropical scincid lizards (Honours). Townsville: James Cook University.
- Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF, 2000. Testosterone, endurance, and darwinian fitness: Natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior* 38:222-233.
- Stamps J, 1977. Social behaviour and spacing patterns in lizards. In: *Biology of the Reptilia Vol. 7* (Gans C, Tinkle DW, eds). London: Academic Press; 265-334.
- Stamps JA, Krishnan VV, 1994. Territory acquisition in lizards: II. Establishing social and spatial relationships. *Animal Behaviour* 47:1387-1400.
- Stamps JA, Krishnan VV, 1998. Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. *Animal Behaviour* 55:461-472.
- Whittier JM, Martin J, 1992. Aspects of social behaviour and dominance in male rainbow skinks, *Carlia rostralis*. *Australian Journal of Zoology* 40:73-79.
- Wilcox D, Dove B, McDavid D, Greer D, 1996. UTHSCA Image Tool for Windows. In, 2.00 ed. San Antonio, Texas: The University of Texas Health Science Centre in Antonio.