Landsc Ecol (2024) 39:139
https://doi.org/10.1007/s10980-024-01935-8

BRIEF COMMUNICATION

Climate change may impact habitat complementation and cause disassociation for mobile species

Nicholas L. James · Graeme S. Cumming

Received: 4 April 2024 / Accepted: 29 June 2024 / Published online: 30 July 2024

Abstract
Context As complementary terrestrial and aquatic habitats are pulled apart by environmental change, animals will have to adjust their behaviours to successfully track their fundamental niches. We introduce a novel example of how climate change impacts can drive separation between complementary foraging and breeding habitats in seabirds.
Objectives We evaluated how Black Noddies (*Anous minutus*) modified their movement behaviour across the seascape to access complementary habitat types during a period of local food scarcity; and whether this influenced their breeding success.
Methods We quantified characteristics of foraging behaviour relating to energy consumption (time, distance and area covered) over four breeding seasons for Black Noddies (*A. minutus*) and compared favourable years (2019, 2020 and 2021) to an unfavourable year (2022). We also quantified and compared chick health and survival rates over the same period.
Results In 2022, severe reduction in local food abundance on Heron Island led breeding Black Noddies to forage further by an order of magnitude, utilizing a remote wooded island (Bushy Islet) as an overnight roosting location. This was a novel and completely unexpected response to the altered environmental conditions. At the same time, 2022 saw significant increases in chick mortality and decreases in chick health compared to other years.
Conclusions We show how a growing mismatch between nesting, roosting, and foraging sites pushed individuals in a breeding tropical seabird population to extend their foraging range by an order of magnitude, with direct negative consequences for juveniles. Our findings highlight the need to explicitly consider habitat complementation in land- and seascape conservation initiatives and planning.

Keywords Adaptive capacity · Breeding success · Foraging behavior · Landscape complementation · Oceanographic processes · Seabirds

N. L. James (✉) · G. S. Cumming
College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia
e-mail: nicholas.james@my.jcu.edu.au

N. L. James
The Great Barrier Reef Marine Park Authority, Townsville, QLD 4811, Australia

G. S. Cumming
Oceans Institute, University of Western Australia, Perth, WA 6009, Australia

Introduction

As Earth's ecosystems undergo increasingly rapid change due to global heating, the survival of many animal populations will depend on their ability to track suitable habitat. Suitable habitats are defined as landscapes that provide access to a full range of critical resources (e.g., for food, shelter, and reproduction). Habitats that contain all essential resources within an accessible distance of each other exhibit habitat complementation (Dunning et al. 1992; Colding 2007; Pope et al. 2000). Although landscape ecologists have recognised that climate change may impact habitat complementation (Heinle et al. 2021), most studies of climate change impacts have focused on access to single resources or habitats and few have documented the potential for climate-driven separation of complementary resources. This latter phenomenon, which we term 'habitat disassociation', has received little direct academic attention in landscape ecology research on species responses to climate change. We thus have limited knowledge of how habitat complementation may change in a warming planet, or of how to manage populations responding to habitat disassociation.

Organisms that rely on particular static features of their local environment, such as caves or islands, seem particularly vulnerable to habitat disassociation. For example, bats that hibernate in caves in cold climates are vulnerable to the loss of adjacent wetlands that they depend on for winter foraging habitat (Mas et al. 2022); and many wetland species require complementary habitats in the wetland-adjacent matrix (Pope et al. 2000). Well-documented empirical examples are urgently needed to illustrate the range of contexts in which habitat disassociation may threaten populations. Incorporating complementary habitats into conservation requires a holistic approach that considers the habitat and interaction needs of species. Preserving complementation can contribute to increased biodiversity, resilience, connectivity and ecological services.

In this manuscript we present a previously undocumented example of how climate change may reduce habitat complementation for seabirds by disassociation of breeding, roosting and foraging locations. We collected telemetry data for Black Noddies (*Anous minutus*) at one of the largest breeding colonies of this species, on Heron Island in the Southern Great Barrier Reef, across four breeding seasons. We also collected additional data on Black Noddy breeding success and offspring mortality. Black Noddies forage on small pelagic fish, which they carry in their crops to feed their young. They breed colonially on wooded islands, where they build leaf nests in suitable trees. Prey fish abundance near the ocean's surface appears to be reduced by warmer water (Devney et al. 2010). In years where fish abundance is lower, Black Noddies must fly further to locate schools of suitably sized fish.

Materials and methods

We used GPS telemetry and regular measurements of chick body mass and head and culmen length to understand how Black Noddies use complementary resources across seascapes. Specifically, we investigated the relationship between the distances that breeding adults travelled and their breeding success (chick condition and mortality). Comparisons were made between breeding seasons across four different years.

To collect data on foraging behaviour we fitted GPS tracking devices to foraging Black Noddies that were actively provisioning offspring in the Heron Island colony in the southern Great Barrier Reef. Trackers (*Lotek PinPoint50* gps device, <3 g) were attached to hand caught individuals (Table 1). We programmed GPS trackers to record locations every 10 min with a mean deployment time of 62.27 ± 11.89 h. Each individual was fitted with a GPS logger only once; all tagged birds were banded and could subsequently be individually identified. After four days or more the tracker was retrieved by recapture of the individual to download data. Chicks provisioned by a tracked adult were weighed and measured for tarsus, culmen and head lengths. The same data were also collected for control nests where no adults were tracked or handled in 2021 and 2022

Table 1 Tracking and chick mortality data

Year	Trackers retrieved	Trackers deployed	Control nests	Chick mortality
2019	4	11	0	7/*
2020	20	31	0	9/*
2021	21	30	10	1/0
2022	7	13	16	7/6
Totals	52	85	26	

Summary of data collected for each nest with a GPS tracked parent or control on Heron Island from 2019 to 2022

Chick mortality values are given separately for both chicks of birds carrying GPS trackers and chicks from control nests, respectively

*Indicates where data was not collected

(Table 1). Chick mortality was recorded where a chick was found dead at the nest or was no longer present on the nest during daily observations.

To investigate changes in foraging behaviour across the seascape, we used a Hidden Markov Model to identify foraging locations. Given that distance travelled from breeding colony is a well-established proxy for energy expenditure, we calculated the total trip distance (between visits to the colony) and distance to each foraging location from the colony (Heron Island). We then used a Wilcox test to detect changes in foraging distances from the colony per year.

We used a Generalised Additive Mixed Model (GAMM) to model chick weight against the combined length of head and culmen measurements for each chick in 2021 and 2022 (Congdon 1990; Devney et al. 2010). Combined head and culmen length was used as a fixed effect while year and individual were used as random effects to account for repeated measures of the same individual and variance in chick weights between years. We extracted the residuals from the fitted model and compared them between years to determine if a significant difference in weight could be detected for the same head and culmen measurements, indicating arrested growth.

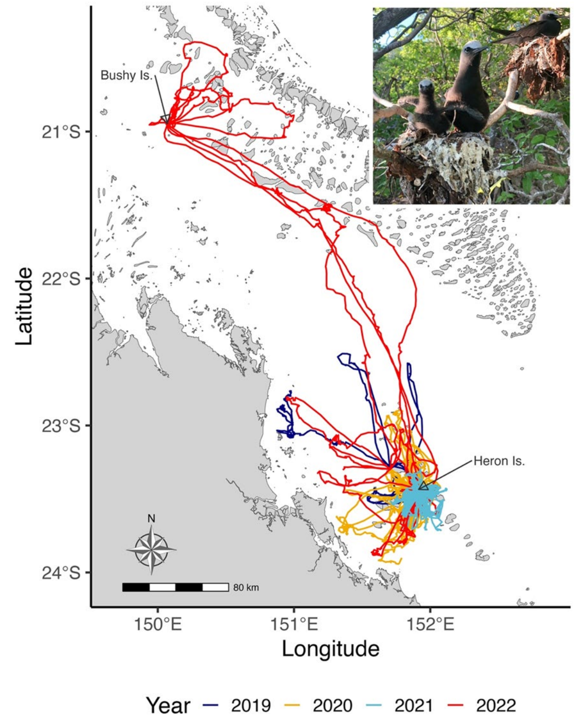
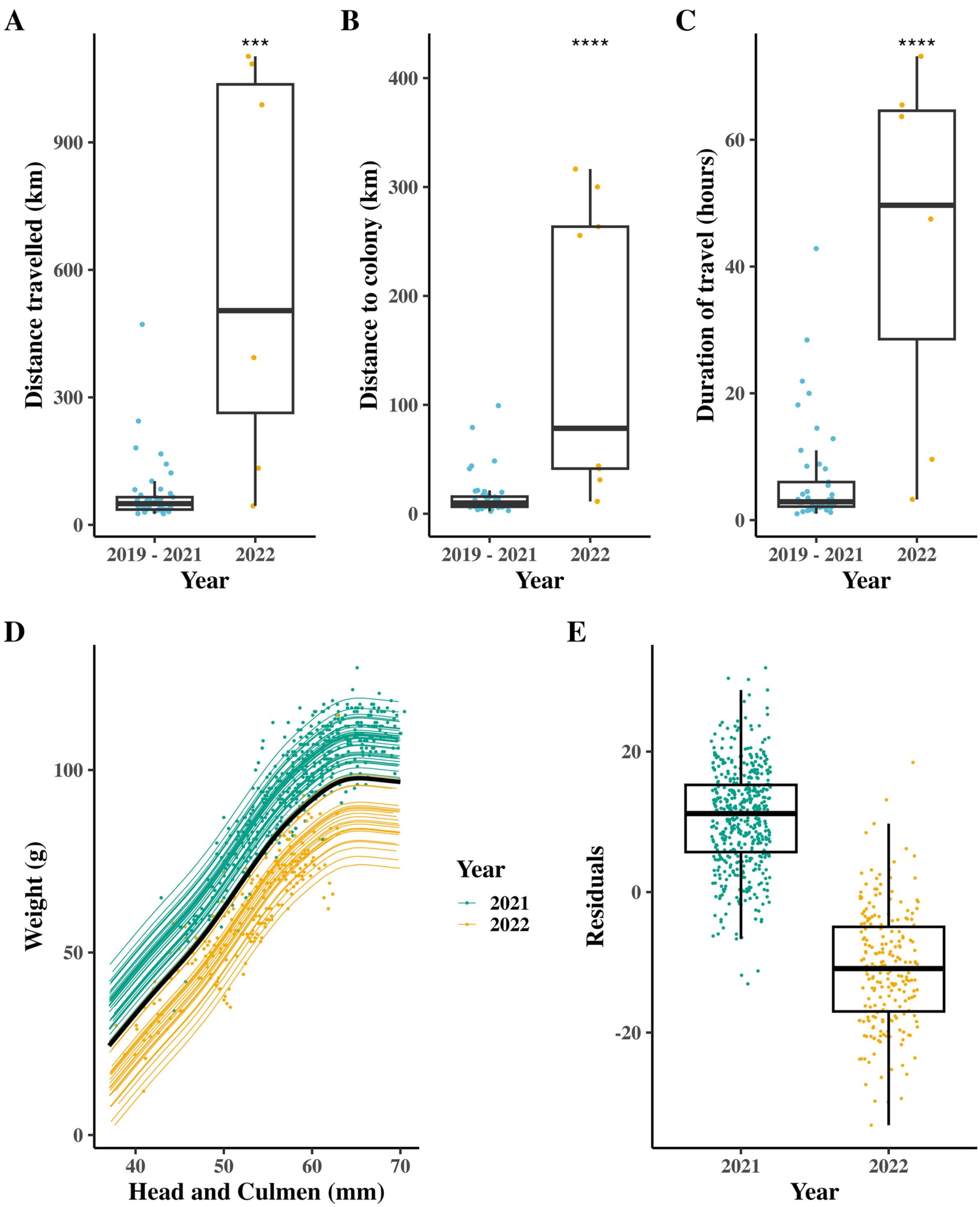


Fig. 1 Foraging tracks of chick-rearing Black Noddies (*Anous minutus*) from years 2019 to 2022 during their December breeding season. Southern Great Barrier Reef, Australia

Results

We had previously observed some inter-annual variance in food availability to breeding Black Noddies at Heron Island, with good years and bad years. In 2022, however, environmental conditions appear to have led to a severe reduction in local food abundance, decoupling breeding locations from foraging locations (Fig. 2A–D). Black Noddies with chicks responded to this decline by foraging further, as might be expected. What we did not expect was that the distances they moved increased by an order of magnitude further than any previously documented foraging trip (Figs. 1, 2A–C). This sudden scale-jump in foraging behaviour appears to have been associated with the use of one of the nearest well-treed northern islands, Bushy Islet, as an overnight roosting location during long foraging trips. Thus, the unusual environmental conditions reduced the complementation of breeding, foraging and roosting sites, forcing birds to respond by using the seascape in what appeared to be a novel and seemingly counter-intuitive way.

In 2019 and 2022, the two seasons with greater foraging distances from the colony, mortality was 54–64%. From 2021 to 2022, mortality in chicks from tracked parents increased from 0.3 to 54% and mortality in control nests increased from 0 to 38%, coinciding with a magnitude increase in foraging distances. Mean trip distance was significantly longer in 2022 (607.3 km ± 450.1) compared to previous years (71.5 km ± 75.5), meaning far greater lengths of time were spent away from the colony in 2022 (44.6 h ± 27.6) compared to 2019–2021 (0.3 h ± 8.3). We also found that chick condition (weight at the same stage of development) was significantly lower in 2022 than in 2021 (Fig. 2). We confirmed that the extracted residuals grouped by year were significantly different with a t-test ($t = 33.373$, $df = 380.12$, $p < 0.001$) with a mean positive value for 2021 (points above the trend line) and negative for 2022.


A
B
C
***
****
****
Distance travelled (km)
Distance to colony (km)
Duration of travel (hours)
2019 - 2021
2022
Year
D
E
Weight (g)
Head and Culmen (mm)
Year
2021
2022
Residuals

◂**Fig. 2** Foraging effort and responses in chick condition. **A** Foraging distances per foraging trip (distance travelled while away from the breeding colony). **B** foraging distance from the colony during breeding season for Black Noddies (*Anous minutus*) from the Heron Island colony, 2019 to 2022. **C** Time duration of foraging trips (time spent away from the breeding colony in a continuous span). Asterisks indicate results from a Wilcoxon's test indicating significantly different foraging patterns in 2022 compared to the reference years 2019–2021. All points represent average values per individual. **D** Prediction plot for the GAMM model of chick weights at measured head and culmen lengths for each year. Points represent observed data. Black line indicates the predicted trend without inter-annual or inter-individual variance. E. Residuals taken from the GAMM per year. The distribution of residuals was found to be significantly different ($t = 33.373$, $df = 380.12$, $p < 0.001$)

Discussion

Our results provide strong evidence for the importance of considering animal responses to climate change as a land- or seascape ecology problem. As one of the first tracking studies on Black Noddies, our findings imply that seabird populations on the GBR may already be subject to changes in oceanographic and/or trophic processes that alter seasonal peaks in prey populations, separating key resources across the seascape and posing a threat to Black Noddy persistence. Black Noddies demonstrate habitat complementation that is limited in environmental and geographical space (Ramiadantsoa et al. 2018). Environmentally, they require sufficient prey abundances, reef matrix foraging grounds and islands with trees for roosting. Geographically, they require these locations to be within daily trip distances from the nest to sustain net positive energy budgets. Disassociation occurs where environmental conditions in one or more habitat types are no longer satisfied, requiring unsustainable levels of effort in order to re-establish access to all complementary habitat types. Species faced with this situation may respond as observed for noddies (significant changes in movement behaviours and broader use of the land- or seascape) but other species may switch resources (e.g. other prey types or roosting habitat) or be unable to adapt.

Prey availability for Black Noddies varies with ocean temperatures and bathymetry (Devney et al. 2010). These variables interact with oceanographic processes that directly influence regional upwellings, which in turn promote primary production and aggregations of seabird prey. For surface-feeding species such as noddies, a deep thermocline puts prey out of reach. Although we could not establish a direct link to environmental covariates, the world's oceans were shifting to an El Niño oscillation at the time of study and the same precursors of change in ocean dynamics may have impacted Black Noddy prey (Devney et al. 2009).

Where specialisation occurs in multiple regions of a species' environmental space, increased susceptibility to habitat association may occur under environmental change (Batáry et al. 2021). Hence, species that have multiple specialist requirements should be at greater risk of disassociation. Further, categorising those requirements by whether they require gradual or immediate responses (e.g. gradual air temperature shifts versus decreased prey availability) and consideration of movement motivations, as for species that return to cached offspring or travel with young, may also help to identify vulnerabilities to disassociation via biological or life stage traits. Similarly, consideration of life history traits may also identify vulnerable species such as those with high offspring investment. Collectively, these considerations should help managers to better predict how populations will respond to climate change and allow for better mediation strategies at appropriate scales.

Our findings contribute new knowledge for consideration in management practices. For example, it is noteworthy that these tropical birds of the southern oceans went further north, rather than further south, to find both prey and suitable roosting locations. Discussions around tropicalisation of the world's ecosystems often assume that tropical species will migrate towards the poles to avoid warmer conditions (Vergés et al. 2019). These assumptions typically ignore the need for complementary habitats; even for fish, cooler water is not necessarily accompanied by suitable breeding or sheltering habitat. Thus, tracking cooler temperatures will not always be the driving force in a population redistributing in response to climate change effects. For management situations where scarce resources are vital to specialist use by an at-risk population, consideration of habitat disassociation may help to predict what resources are important and how dependence on them may change across land- and seascapes.

Climate driven habitat disassociation deserves considerably more attention in landscape ecology research on climate change and its impacts on population and community ecology, as well as in conservation planning. Access to resources within a land- or seascape is context specific, being primarily driven by habitat spatial arrangement and composition (Dunning et al. 1992) relative to the traits of organisms (e.g., mobility and resource needs) (Gaigher et al. 2021). Studies in behavioural plasticity typically consider how novel behaviour influences the capacity of populations to overcome changes in resource availability and environmental cues (Schmitz and Barton 2014; Bonamour et al. 2019; Ducatez et al. 2020), but not the role of access to complementary habitats. Our research unites these areas of study by showing how adaptive capacity can also be affected if obligatory access to specific static resources excludes habitat beyond the movement capacity of individuals. Disparate range and phenological shifts within communities (Thackeray et al. 2010; Marske et al. 2023) will further increase the chances of habitat disassociation in populations using static resources. Consideration of these concepts together, as demonstrated in this study, suggests new and exciting avenues for understanding and managing the impacts of climate change on biodiversity.

Acknowledgements This research was supported by the ARC Centre of Excellence for Coral Reef Studies and James Cook University. We are grateful to Bradley Congdon for his intellectual contributions to this study. We also thank Bradley Congdon, Emma Carmichael and Penn Lloyd for their assistance with field work on Heron Island.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Nicholas L. James and Graeme S. Cumming. The first draft of the manuscript was written by Nicholas L. James and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. The work was supported by The Australian Research Council's Centre of Excellence for Coral Reef Studies and a Western Australia Premier's Science Fellowship awarded to GSC.

Declarations

Conflict of interest The authors have no competing interests to declare.

Ethical approval All work is original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal. No part of the research has been published in any form elsewhere. The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal. All sources of funding are acknowledged in the manuscript. All appropriate ethics and other approvals were obtained for the research. Work was authorised under the Department of Environment and Science Permit PTU19-001332, Australian Bird and Banding Scheme Authority Numbers 1386 and 3395 and James Cook University Ethics Approval A2592.

References

Batáry P, Rösch V, Dormann CF, Tscharntke T (2021) Increasing connectivity enhances habitat specialists but simplifies plantinsect food webs. Oecologia 195:539–546. https://doi.org/10.1007/s00442-020-04830-6

Bonamour S, Chevin L-M, Charmantier A, Teplitsky C (2019) Phenotypic plasticity in response to climate change: the importance of cue variation. Phil Trans Royal Soc b: Biol Sci 374:20180178

Colding J (2007) Ecological land-use complementation for building resilience in urban ecosystems. Landsc Urban Plan 81:46–55

Congdon BC (1990) Brood enlargement and post-natal development in the black noddy *Anous Minutus*. Emu—Austral Ornithol 90:241–247

Devney CA, Short M, Congdon BC (2009) Sensitivity of tropical seabirds to El Niño precursors. Ecology 90:1175–1183

Devney CA, Caley MJ, Congdon BC (2010) Plasticity of noddy parents and offspring to sea-surface temperature anomalies. PLoS ONE 5:e11891

Ducatez S, Sol D, Sayol F, Lefebvre L (2020) Behavioural plasticity is associated with reduced extinction risk in birds. Nat Ecol Evol 4:788–793

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169

Gaigher R, Pryke JS, Samways MJ (2021) Habitat complementarity and butterfly traits are essential considerations when mitigating the effects of exotic plantation forestry. Biodivers Conserv 30:4089–4109

Heinle KB, Eby LA, Muhlfeld CC, Steed A, Jones L, D'Angelo V, Whiteley AR, Hebblewhite M (2021) Influence of water temperature and biotic interactions on the distribution of westslope cutthroat trout (*Oncorhynchus clarkii* lewisi) in a population stronghold under climate change. Canadian J Fisheries Aquatic Sci 78(4):444–456

Marske KA, Lanier HC, Siler CD, Rowe AH, Stein LR (2023) Integrating biogeography and behavioral ecology to rapidly address biodiversity loss. Proc Nat Acad Sci 120(15):e2110866120

Mas M, Flaquer C, Puig-Montserrat X, Porres X, Rebelo H, López-Baucells A (2022) Winter bat activity: The role of wetlands as food and drinking reservoirs under climate change. Sci Total Environ 828:154403

Pope SE, Fahrig L, Merriam HG (2000) Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81(9):2498–2508

Ramiadantsoa T, Hanski I, Ovaskainen O (2018) Responses of generalist and specialist species to fragmented landscapes. Theor Popul Biol 124:31–40

Schmitz OJ, Barton BT (2014) Climate change effects on behavioral and physiological ecology of predator-prey interactions: Implications for conservation biological control. Biol Control 75:87–96

Thackeray SJ, Sparks TH, Frederiksen M et al (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Change Biol 16:3304–3313

Vergés A, McCosker E, Mayer-Pinto M, Coleman MA, Wernberg T, Ainsworth T, Steinberg PD (2019) Tropicalisation of temperate reefs: Implications for ecosystem functions and management actions. Funct Ecol 33(6):1000–1013