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Short Communication

Variable choice affects estimations of vulnerability to climate change

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For practical reasons, assessments of species' vulnerability to rising temperatures are often limited to measuring responses to a single ecological response variable, but this could result in an underestimation of vulnerability. Using the Cape Rockjumper *Chaetops frenatus* ('Rockjumper') we examined the thermal risk to nestling Rockjumpers for sublethal (i.e. reduced nestling mass gain) and lethal (i.e. increased nest predation) consequences of sustained hot weather under both current and predicted future climatic conditions (RCP 8.5). We used a direct approach to examine these risks, first as independent ecological responses and then as combined risk driven by both response variables (mass gain and predation risk). This study revealed that the inclusion of multiple climate-related responses affected the predicted vulnerability to climate change. Further, our analyses showed that increased vulnerability to climate change will vary within the Rockjumper's habitat. Our results demonstrate that the variability in predicted thermal risk depends on which response variable was used, with implications for how and where conservation practitioners direct their already limited resources.

Keywords: climate change, ecological interactions, mechanistic modelling, species vulnerability, thermal risk.

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Over recent decades, many consequences of climate change have been documented and studies continue to show the profound threat that climate change poses to biodiversity globally (Chapin *et al.* 2001, Bellard *et al.* 2012, Weiskopf *et al.* 2020). Thus, there is intensifying interest in assessing how climate change may affect species' distributions, survival and population persistence (e.g. Biggs *et al.* 2008, Bellard *et al.* 2012, Bonebrake *et al.* 2018, Freeman *et al.* 2018). In recent years, process-explicit modelling approaches have increasingly been used to determine species exposure to climate-related risks (e.g. Mathewson *et al.* 2016, Albright *et al.* 2017, Conradie *et al.* 2019, 2020, Riddell *et al.* 2021, Ma *et al.* 2023). However, probably for reasons of practicality, many of these studies consider only a single aspect of species' sensitivity or response to increasing air temperatures (T_{air}) when estimating vulnerability to climate change.

By including only a single response variable, climate vulnerability models may underestimate risks associated with other dimensions of a species' biology. For example, many studies focus on physiological responses to high T_{air} (e.g. body temperature, water loss; Albright *et al.* 2017, Riddell *et al.* 2019), with less attention focused on behavioural and ecological limitations of species responses (but see Conradie *et al.* 2019). Here, we present a simple but clear example of how including multiple behavioural and ecological responses to high T_{air} can provide a more nuanced insight into future threats associated with rising T_{air}.

We used the Cape Rockjumper *Chaetops frenatus* ('Rockjumper') as a case study, a South African mountain-endemic with multiple life-history traits associated with vulnerability to climate change (see review in Pacifici *et al.* 2015). These life-history traits include specialized habitat (restricted to the rare Mountain Fynbos biome) and restricted distribution (Lee & Barnard 2016), in addition to limited thermal tolerance (Oswald *et al.* 2018b, 2020b). Further, multiple studies have indicated additional aspects of Rockjumper ecology (specifically aspects of their nesting ecology) that make them vulnerable to high T_{air}. For instance, over prolonged periods of exposure to high T_{air}, sublethal fitness costs may arise due to behavioural trade-offs through decreased parental foraging effort (Oswald *et al.* 2019) or the inability of parents to accommodate for higher juvenile water and energy demands at high T_{air} (Oswald *et al.* 2018a). Moreover, a recent population viability analysis found that any increase in mortality of young Rockjumpers could strongly impact population persistence (Oswald & Lee 2021).

Here, we quantified the effects of rising T_{air} on Rockjumper ecology and survival using a combination of behavioural, ecological and geospatial temperature data to inform a mechanistic model. Further, we tested how predictions of thermal vulnerability vary for a single species when using a single ecological variable compared with the inclusion of multiple variables. We created 'vulnerability assessment maps' of exposure to the adverse effects of high T_{air} based on two Rockjumper nest success variables (first separately and then combined). These maps highlighted the change in the number of days where Rockjumper nestlings are vulnerable to (1) reduced nestling mass gain (consecutive number of days with daily maximum T_{air} > 22.4 °C), (2) increased predation risk (total number of days with daily maximum T_{air} > 25 °C) and (3) combined risk where nestlings are at risk of both reduced mass gain and increased predation risk under current conditions and a predicted future climate change scenario (RCP 8.5, business-as-usual).

METHODS

Study species

The Rockjumper is an endemic species found solely in the Mountain Fynbos sub-habitat within the Cape Floristic Region (Lee & Barnard 2016). The Cape Floristic Region is a small vegetative belt (~90 000 ha) of heathland found in the southwest corner of South Africa and is the smallest of the six globally recognized floral kingdoms. The Cape Floristic Region is one of five Mediterranean-type biomes across the planet, all considered biodiversity hotspots, and all of high conservation concern due to climate change (Sala *et al.* 2000, Simmons *et al.* 2004). In 2017, Rockjumpers were assessed as Near Threatened by the IUCN (IUCN 2017). Rockjumper habitat and reporting rates have experienced localized declines (25% in range and 53.4% in reporting rate) over the past three decades (Lee *et al.* 2017) but are not declining in areas of their habitat where climate has remained stable over this time (Milne *et al.* 2015). Further, Rockjumpers fulfil multiple criteria necessary to be considered an indicator species for the adverse effects of climate change (see Carignan & Villard 2002). For instance, they occur only on continental sky islands (McCormack *et al.* 2009), are probably climate relicts (Woolbright *et al.* 2014), and they show a high degree of habitat specialization and restriction, in common with many mountain endemics (Scridel *et al.* 2018, de Zwaan *et al.* 2022). Additionally, they appear unable to shift their range if current habitat becomes thermally unsuitable (Kupfer *et al.* 2005), and their Mountain Fynbos habitat is at high risk of size reduction from climate change (Simmons *et al.* 2004). Finally, we chose Rockjumpers as our focal species as data are available for temperature thresholds at which the breeding ecology and survival of Rockjumpers become adversely affected (see overview Box 1).

Vulnerability assessment

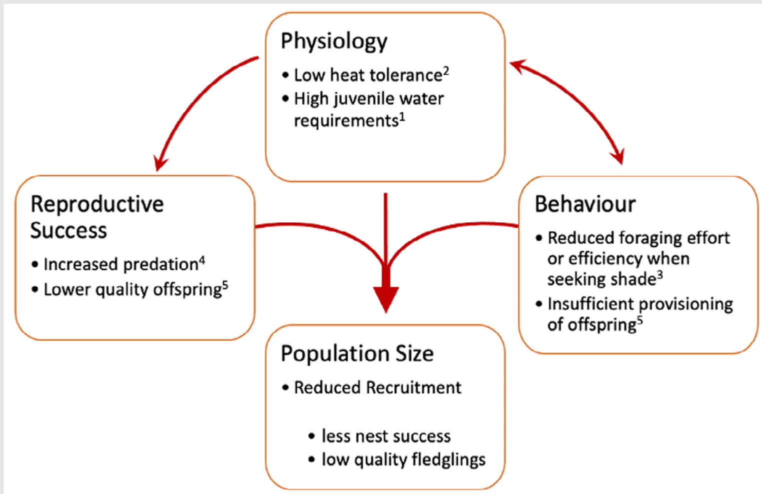
We created vulnerability assessment maps following the methods of Conradie *et al.* (2019). In brief, the maps used modelled climate data for current (2000–2014) and future climate conditions (2076–2100). We obtained these data from the National Center for Atmospheric Research (Boulder, CO, USA, https://esgf-node.ipsl.upmc.fr/search/cmip5-ipsl/) to extract daily maximum T_{air} associated with inflection points for increases in sublethal (i.e. reduced nestling mass gain) and lethal (i.e. predation risk) fitness costs in Rockjumpers described below. For current climate conditions, we selected NOAA Cooperative Institute for Research in Environmental Sciences 20th Century Reanalyses (v2c) modelled climate data with forcing fields interpolated to 1.88° latitude × 1.88° longitude (~200 km^2) and recorded daily T_{air} (°C) at an hourly resolution. We created future climate vulnerability maps using the experiment *r6i1p1* RCP 8.5 scenario of the CCSM4 projection from CMIP V (https://cmip.llnl.gov/cmip5/), with forcing fields interpolated to 0.95° latitude (~100 km^2) × 1.25° longitude (~140 km^2). We selected the RCP 8.5 scenario (i.e. business-as-usual, unmitigated climate change projections) as the most likely future scenario because these models best simulate current conditions (Brient *et al.* 2016) and the CCSM4 project forms part of a collaborative project with strong model convergence. We stored both current and future climate data in network common data form (netCDF) and analysed them in the R statistical environment version 3.5.3 (R Core Team 2016) using RStudio version 1.1.463 (RStudio Team 2020, see Conradie *et al.* 2019 for complete details on methodology). We obtained the current distribution range of Rockjumpers from BirdLife International (http://datazone.birdlife.org/) and NatureServe (https://www.natureserve.org/), overlaying the distributions onto the vulnerability assessment maps we created. These distribution ranges were assembled into shape files by BirdLife International and NatureServe from numerous sources including observation and occurrence data, museum records, distribution atlases, surveys and field guides. Additionally, the range map was checked against distribution data from the Southern African Bird Atlas Project 2 (http://sabap2.adu.org.za/).

We used climate data from within the Rockjumpers' breeding season (August to December; Holmes *et al.* 2002) as both of our response variables were based on breeding ecology. We also restricted our analyses of daily maximum T_{air} calculated for each raster cell to daytime (06:00–18:00 h) due to the diurnal nature of both response variables: nestling mass data were collected during the day (Oswald *et al.* 2021) and snake predation was predominantly diurnal (n = 1 of 19 predation events may have been nocturnal; Oswald

Box 1 Overview of previous research on Cape Rockjumpers *Chaetops frenatus* showing areas of temperature sensitivity and their interacting effects.

Box 1 Interacting Effects of Responses to Increasing Temperature

Recent studies examined the effects of increasing temperatures on the Cape Rockjumper *Chaetops frenatus.* While no single study was conclusive in determining why Rockjumper populations were declining in warming areas of their habitat, several showed potential areas of vulnerability. Decreasing populations are likely due to a combination of biological interactions. For example, reduced mass gain for nestlings at high temperatures may be due to a



decrease in parental foraging efficiency (i.e. a combination of behavioural changes and reproductive success), or because parents cannot increase provisioning rates to accommodate for high nestling water and energy demands (i.e. a combination of behavioural changes and physiological demands). As nest predation itself increases at higher temperatures, these interactions may be exacerbating one another and resulting in a reduction of overall Rockjumper population size.

(Oswald et al., 2018a[1], 2018b[2], 2019[3], 2020a[4], 2021[5])

et al. 2020a). We created vulnerability assessment maps for the following scenarios: (1) longest period of consecutive number of days where daily maximum T_{air} > 22.4 °C and nestlings were likely to have reduced mass gain, (2) total number of days where daily maximum T_{air} > 25 °C and there was increased risk of nest predation from snakes, and (3) both longest period of consecutive number of days with daily maximum T_{air} > 22.4 °C and total number of days with daily maximum T_{air} > 25 °C. To examine the combined risk (i.e. days where both risks are present), we selected six sites across the Rockjumper's range (north-west, north-central, north-east, south-west, south-central, south-east) by selecting single raster cells closest to the centre of each site, representing interpolated climatic conditions over ~200 km^2. For effects on nestling mass gain, we used the total number of consecutive days as opposed to simply the total number of days as the effects of reduced mass loss are additive (Gardner *et al.* 2017).

RESULTS

In the high-risk future climate change scenario, the total risk of T_{air} having negative effects on nestling mass gain and nest predation increased in both frequency and geographical extent (Fig. 1). The risk of reduced nestling mass gain and increased nest predation also varied across the geographical range (i.e. some areas of their range would see a greater increase in risk days than others; Fig. 1), with a notable increase in number of risk days

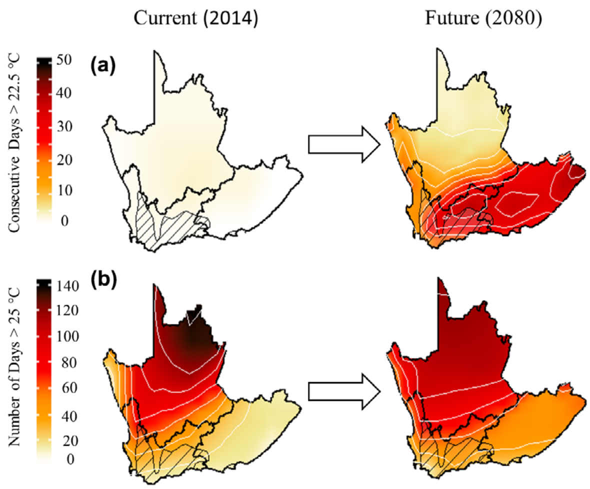


Figure 1. (a) Consecutive number of days per breeding season (August to December) when nestling Cape Rockjumpers *Chaetops frenatus* have reduced daily change in mass (i.e. days > 22.5 °C). (b) Total number of days per breeding season (August to December) with greater probability of nest predation (i.e. days > 25 °C). Maps show risk assessment under current conditions (2000–2014; 'Current (2014)') and a future scenario (RCP 8.5; 2080–2090; 'Future (2080)'). Current range for Rockjumpers is indicated with cross-hatching.

from the northern locations compared with those further south (Fig. 2). For example, for our north-central location, the number of consecutive days where nestlings were exposed to T_{air} > 22.4 °C increased ~30 days by 2080 (Fig. 2a) compared with an increase of ~20 days in our south-central location (Fig. 2e).

Overall, the additive effect of including both variables (consecutive number of days T_{air} > 22.4 °C and number of days T_{air} > 25 °C) revealed a greater total risk of exposure to the negative consequences of high T_{air} than if each variable was examined separately. Areas typically experiencing hotter weather (i.e. northern and inland sites) currently experience sporadic hot days, but by 2080 are predicted to be exposed to >90 days with T_{air} > 25.0 °C, with up to 72 of those days consecutively exceeding T_{air} > 22.4 °C. Specifically, the greatest increase in number of risk days will be in the north-west section of the Rockjumper's range, where the total number of days that nestlings may be at risk of either reduced mass gain or increased predation will increase from ~20 to ~150 days (Fig. 2a).

DISCUSSION

Investigating species responses to increasing temperature is important for predicting the probable impacts of climate change on species in the near future, but choosing which response variable to include in predictive models can be challenging. Given that we included only two temperature-sensitive variables, the difference in our results depending on which variable was examined has far-reaching consequences for conservation management. We also found significant differences when examining each variable independently compared with examining the combined effects of both variables, further demonstrating the importance of including multiple variables in such analyses. There could be far-reaching implications for conservation and resource allocation, considering we found geographical variation in our vulnerability assessment maps depending on the chosen response. For example, while one variable would see resources focused on the north-west (where nestling mass gain is predicted to have the highest increase in risk), the other would see them focused on the east (where the risk of nest predation is predicted to have the highest increase). We can only assume that if more variables and aspects of climate sensitivity were included in our overview, the results would further underscore the necessity for including as much information as possible to make the most accurate predictions of vulnerability and decisions on where to focus conservation efforts.

Limitations of the study

We do want to highlight four main caveats of this study to be considered for future vulnerability assessments. First, our two chosen variables related to effects at the nest and are likely to be synergistic at higher temperatures. Indeed, in Oswald *et al.* (2021) the effects of temperature on mass gain became difficult to model above ~30 °C, as nests experienced high rates of predation and few survived on days with these T_{air}. Secondly, many species (including Rockjumpers) often use behavioural or physiological adjustments to cope with higher temperatures, and our spatial resolution may disregard the potential effects of cooler microsites. However, previous studies have shown that the use of microsites itself could have negative consequences for provisioning, and thus would also negatively affect the nestling mass gain metric used in the current analysis (Box 1). Thirdly, although the current analysis was based purely on considering our two variables as additive, we hope this may lead future studies to investigate the potential for interactive effects, leading to even more nuanced vulnerability assessments. Finally, while we showed the benefits of including multiple biotic variables when creating vulnerability assessments, it is probably as important for studies to consider including multiple abiotic variables.

Conservation implications

We not only highlight the importance of including multiple variables in vulnerability models, but also of

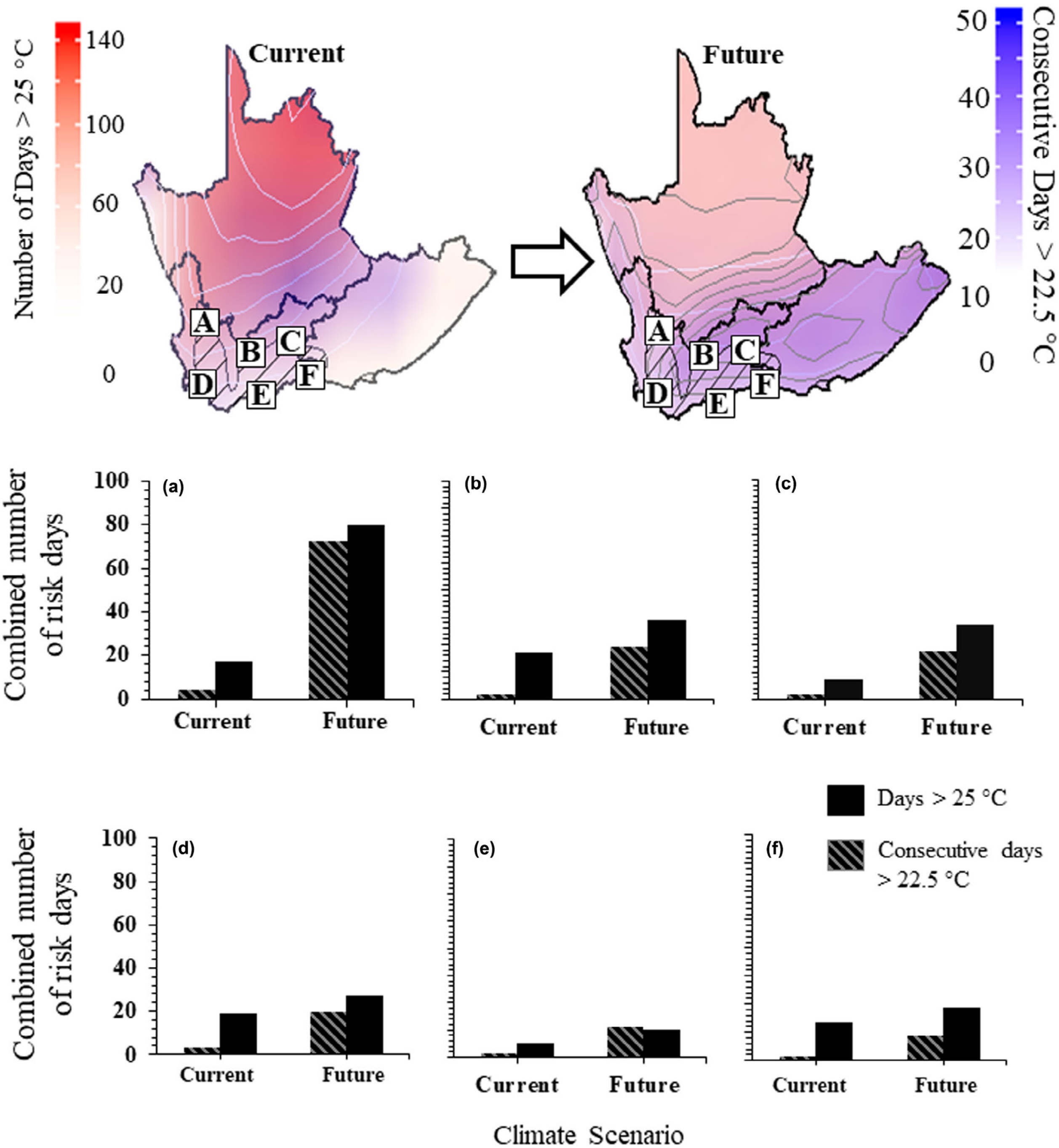


Figure 2. Number of days where Cape Rockjumpers *Chaetops frenatus* could experience both reduced nestling mass gain (grey cross-hatching) and increased nest predation (black) under current conditions (2000–2014) and predicted future climate scenario (RCP 8.5; 2080–2090) from across the Rockjumper's current range (a – north-west, b – north-central, c – north-east, d – south-west, e – south-central, and f – south-east).

identifying areas within the current range of species where the impacts of climate change are likely to be severe. For instance, in the north-east corner of their current range, nestling Rockjumpers will experience an increase of ~70 days of increased vulnerability by the last quarter of the century when combining both variables as compared with each variable separately (Fig. 2c), but only ~20 more days in the south-east edge of their current range (Fig. 2f). This suggests possible refugia along the southern coastline, possibly buffered by cooler winds from the Southern Ocean, or from the Fynbos' atypical rainfall for a Mediterranean climate, which can occur in winter or summer depending on the movement of equatorial air (Rebelo *et al.* 2006). We thus emphasize the importance of including multiple aspects of a species' ecology and habitat structure when examining susceptibility to climate change.

While we continue to stress the importance of collecting multi-variable data for determining vulnerability for any species, the vulnerability shown here in the Rockjumper may present important applications for conservation of other species. For example, our results could be used to predict responses for other species inhabiting similar niches (e.g. other range-restricted mountain birds with similar sensitivity to climate change), or our results could be used to predict fine-scale responses of other species restricted to the same habitat (e.g. other Fynbos endemics). In the first instance, examples include Gray-crowned Rosy-Finch *Leucosticte tephrocotis* experiencing extreme breeding habitat loss in North America (Richardson 2003) or the preference of White-winged Snowfinch *Montifringilla nivalis* for foraging at lower T_{air} in Europe (Brambilla *et al.* 2017). In the second instance, the effects of increasing temperatures found for Rockjumpers may also occur for the three other Fynbos endemics ranked among the species most susceptible to climate change in southern Africa – Victorin's Warbler *Cryptillas victorine*, Orange-breasted Sunbird *Anthobaphes violacea* (Simmons *et al.* 2004), and Protea Canary *Crithagra leucoptera* (Milne *et al.* 2015).

Deciphering patterns and outcomes of complex biological interactions is time-consuming and can be expensive, as this requires a large amount of focused data collection and creating multi-variable maps may therefore not always be feasible. As resources for conservation are limited, our findings accentuate how crucial it is to choose appropriate and ecologically meaningful variables when predicting vulnerability to threats such as increasing temperatures. It is thus important to consider collecting fine-scale data on representative species such as those in habitats or areas at risk, as species strongly associated with a particular habitat type can be useful indicators for the habitat itself (Carignan & Villard 2002). Further, this can aid in understanding which areas and/or species should be prioritized in conservation planning and management action.

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AUTHOR CONTRIBUTIONS

Krista N. Oswald: Conceptualization; formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **Shannon R. Conradie:** Formal analysis; methodology; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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None.

Data Availability Statement

All data used in this paper have been published previously and are publicly available at the following DOIs: 10.1111/jav.02756, 10.1111/ibi.12846, 10.2989/00306525.2018.1509905, 10.1007/s10336-018-1582-8, 10.1016/j.anbehav.2019.09.006.

ETHICAL NOTE

None.

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