

Research



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Authors for correspondence:

Henry S. Pollock
e-mail: henry.s.pollock@gmail.com
Ari E. Martínez
e-mail: arimartinez043@gmail.com

†These authors contributed equally to this work.

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Heterospecific eavesdropping in ant-following birds of the Neotropics is a learned behaviour

Henry S. Pollock^{1,2,†}, Ari E. Martínez^{3,†}, J. Patrick Kelley^{4,5},
Janeene M. Touchton⁶ and Corey E. Tarwater⁵

¹Program in Ecology, Evolution, and Conservation Biology, University of Illinois at Urbana-Champaign, 505 S. Goodwin Avenue, Champaign, IL 61801, USA

²Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523, USA

³Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132, USA

⁴Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

⁵Department of Zoology and Physiology, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA

⁶Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panama

HSP, 0000-0002-8698-691X; AEM, 0000-0001-9711-4669

Animals eavesdrop on other species to obtain information about their environments. Heterospecific eavesdropping can yield tangible fitness benefits by providing valuable information about food resources and predator presence. The ability to eavesdrop may therefore be under strong selection, although extensive research on alarm-calling in avian mixed-species flocks has found only limited evidence that close association with another species could select for innate signal recognition. Nevertheless, very little is known about the evolution of eavesdropping behaviour and the mechanism of heterospecific signal recognition, particularly in other ecological contexts, such as foraging. To understand whether heterospecific eavesdropping was an innate or learned behaviour in a foraging context, we studied heterospecific signal recognition in ant-following birds of the Neotropics, which eavesdrop on vocalizations of obligate ant-following species to locate and recruit to swarms of the army ant *Eciton burchellii*, a profitable food resource. We used a playback experiment to compare recruitment of ant-following birds to vocalizations of two obligate species at a mainland site (where both species are present) and a nearby island site (where one species remains whereas the other went extinct approx. 40 years ago). We found that ant-following birds recruited strongly to playbacks of the obligate species present at both island and mainland sites, but the island birds did not recruit to playbacks of the absent obligate species. Our results strongly suggest that (i) ant-following birds learn to recognize heterospecific vocalizations from ecological experience and (ii) island birds no longer recognize the locally extinct obligate species after eight generations of absence from the island. Although learning appears to be the mechanism of heterospecific signal recognition in ant-following birds, more experimental tests are needed to fully understand the evolution of eavesdropping behaviour.

1. Introduction

A central goal in the field of animal communication is understanding how interactions between signal producers and signal receivers influence the evolution of signal recognition [1,2]. Eavesdropping—the reception and use of signals intended for other receivers [3]—is a common behaviour with clear fitness implications. Heterospecific eavesdropping can be particularly beneficial by providing useful information with reduced risk of competition relative to conspecific eavesdropping [4,5]. For example, animals use information obtained

from heterospecific eavesdropping to increase foraging success [6], reduce predation risk [3,4] and identify high-quality habitat patches [7]. The numerous fitness benefits associated with heterospecific eavesdropping coupled with its prevalence among diverse animal taxa suggest that the ability to recognize and respond to ecologically relevant heterospecific signals is subject to strong selection [3,4,8].

Despite the growing body of the literature documenting the importance of heterospecific eavesdropping in animal communication, how animals are able to recognize and respond to signals intended for others is not fully understood. Eavesdropping behaviour may arise through learned or innate signal recognition, although few studies have tested the mechanistic basis of heterospecific eavesdropping behaviour (but see [9,10]), primarily because it is difficult to determine an individual's ecological history [3]. Extensive research on avian mixed-species flocks suggests that birds learn to eavesdrop on alarm calls of heterospecifics to obtain information about predator presence [3,11–14]. By contrast, there is some evidence that animals can innately recognize heterospecific alarm calls that are structurally similar to conspecific alarm calls [15,16] or contain 'frightening' features (see [3] for a review). However, previous studies of the evolution of heterospecific eavesdropping have been limited to the context of brood parasitism [17] or predation risk [12,14]. Animals also use heterospecific eavesdropping to find profitable food resources [18–20], yet the mechanistic underpinnings of this behaviour are unclear.

In this paper, we take advantage of an ecological experiment to determine whether heterospecific eavesdropping behaviour in ant-following birds of the Neotropics is innate or learned. Previous research has indicated that ant-following birds eavesdrop on the vocalizations of a dominant obligate ant-following species (ocellated antbird—*Phaenostictus mcleannani*) to locate army ant (*Eciton burchellii*) swarms, a profitable food resource for many bird species [18,20]. Because of the potential fitness benefits associated with foraging at such a profitable resource [21,22], the ability to find and recruit to ant swarms may be subject to strong selection, favouring the evolution of innate signal recognition of *P. mcleannani*'s vocalizations in heterospecifics. Alternatively, birds may learn to associate the vocalizations of *P. mcleannani* with the presence of an ant swarm through prior ecological experience. To test these contrasting hypotheses, we compared recruitment of ant-following birds to *P. mcleannani* vocalizations at an island site (where *P. mcleannani* went locally extinct in the 1970s) and a mainland site (where *P. mcleannani* remains). As a positive control, we also measured responses of ant-following birds to a subordinate obligate ant-following species, the bicoloured antbird (*Gymnopithys bicolor*), which is present at both the island and mainland sites. The local extinction of *P. mcleannani* provided the opportunity to test whether island birds have the innate ability to recognize and respond to vocalizations of *P. mcleannani*. We made the following predictions: (i) island and mainland ant-following birds would respond to vocalizations of the present obligate ant-following species (*P. mcleannani* and *G. bicolor* on the mainland, *G. bicolor* on the island); and (ii) if eavesdropping is a learned behaviour, mainland birds but not island birds would respond to vocalizations of *P. mcleannani*. Alternatively, if eavesdropping is an innate behaviour, then both mainland and island birds would respond to vocalizations of *P. mcleannani*.

2. Material and methods

(a) Study system

Army ant (*E. burchellii*) swarms are a prominent feature of Neotropical forests. Swarms forage through the leaf-litter and flush terrestrial arthropods *en masse*, attracting a diverse suite of bird species that vary in their attendance at swarms [23]. Obligate ant followers depend entirely on ant swarms for food, facultative ant followers regularly attend swarms but also have well-defined territories, and opportunistic species attend swarms only occasionally when army ants cross their territories [23]. Obligate ant followers spend the preponderance of their time foraging at swarms and exhibit specialized behaviours such as bivouac-checking to find active swarms [24]. Therefore, obligate species are thought to be a reliable indicator of the presence of a swarm. Indeed, previous research has demonstrated that heterospecifics eavesdrop on acoustic vocalizations of obligate ant-following species (including *P. mcleannani* and *G. bicolor*) to locate swarms [18,20].

(b) Sampling localities

We conducted the playback experiment at one mainland locality (Pipeline Road, Panama; hereafter 'mainland') in 2014 and one island locality (Barro Colorado Island, Panama; hereafter 'island') in 2015. We sampled in the dry season (February–March) in both years to control for potential seasonal effects on ant swarm activity. The mainland site is a one-lane gravel road that runs through the 22 000 ha Soberanía National Park, which consists primarily of older secondary lowland moist forest (see [25] for more details). The island site is a 1600 ha remnant of primarily old-growth foothill forest located only 9 km from the mainland site that was formed during the construction of the Panama Canal in the early twentieth century, when thousands of acres of lowland forest were flooded to create the artificial Lake Gatún [26]. Prior to formation, the island bird community was highly similar to the mainland community, but over time numerous species have gone locally extinct [26–28]. *Phaenostictus mcleannani* has not been seen on the island in at least 36 years (7.7 generations, 95% CI: 5.2–9.7 generations; based on estimates of *P. mcleannani* survival from [29] and generation time models from [30,31]), but is still abundant on the mainland [28,32]. Therefore, the island bird community is naive to *P. mcleannani*, providing an opportunity to test whether or not island ant-following birds innately recognize *P. mcleannani* vocalizations.

(c) Experimental design

We conducted playback trials at six points between the hours of 06.00–09.00 local time (when recruitment to ant swarms is highest; H.S.P. 2014, personal observation) at both mainland and island sites. At each site, all six points were located on flat terrain in closed-canopy forest with relatively open understory to facilitate identification of birds recruiting to playbacks. Points were separated by greater than or equal to 500 m to ensure spatial independence and reduce the probability of re-sampling the same individuals at each point. At the mainland and island sites, all points were located at least 200 m from the road or island edge to control for potential edge effects on recruitment to playbacks. At each point, we exposed ant-following birds to three playback types in randomized order: (i) vocalizations of *P. mcleannani* (obligate ant-following species present on the mainland but absent from the island); (ii) vocalizations of *G. bicolor* (a positive control obligate ant-following species which is present at both sites and has been shown to elicit positive responses from ant-following birds on the mainland); and (iii) vocalizations of blue-black grosbeak (*Cyanocopsa cyanooides*)—a negative control species that does not regularly attend ant swarms and is present

at both sites). Because our previous research indicated that flock size was an important factor influencing recruitment to swarms [20], we exposed birds to playbacks simulating small (two individual) and large (eight individual) flock sizes for each of the three treatments. Overall, the total number of playback trials in the experiment for the three treatments and two group sizes at six replicate points was $3 \times 2 \times 6 = 36$ trials. We only presented one playback per day at each of the six experimental points.

(d) Playbacks

To create the playbacks, we obtained recordings (in WAV format) of the vocalizations of the three focal species (*P. mcleanmani*, *G. bicolor* and *C. cyanoides*) using archives at the Cornell Lab of Ornithology's Macaulay Library (www.macaulaylibrary.org), as well as personal recordings from individuals (K. Allaire, A. Kirschel, J.P.K. and C.E.T.). Because geographical variation in vocalizations is common among birds, including antbirds [33] (J.P.K. and C.E.T. 2014, unpublished data), we restricted the sound files that we used for playbacks to individuals that were recorded within Panama and Costa Rica, including only song and call variants that we had previously heard at both island and mainland field sites (H.S.P., J.P.K. and C.E.T. 2014, personal observations). Additionally, we confirmed that preliminary playback experiments reliably elicited conspecific responses from the present obligate species at both island and mainland sites (H.S.P. and C.E.T. 2014, personal observations).

We used the sound software program REAPER (v. 4.581, 2014) to simulate the playback of multiple individuals vocalizing simultaneously by manually creating and overlaying either two or eight tracks for each recording. To control for pseudo-replication, we used 8–10 different exemplars of each species to create six unique playback recordings for each treatment. We randomly selected recordings of either two (for the small flock size playbacks) or eight (for the large flock size playbacks) individuals from the available pool of exemplars for each species and combined the tracks in a randomized order for each of the six playback trials per treatment. Playbacks contained a combination of calls and loudsongs (see electronic supplementary material, figure S1 for vocalization spectrograms) typically used in agonistic interactions at swarms, and vocalization rates for individuals of each focal species were designed to emulate as closely as possible the acoustic environment at a swarm and were based on previous observations of vocalization rates at multiple swarms (J.P.K. and C.E.T. 2014, personal observations).

We filtered all recordings below 0.5 kHz to remove low-frequency background noise and removed the vocalizations of other bird species that could confound the interpretation of the target signal. All files were saved at 24-bit rate and 44 000 Hz. We equalized recordings to the same amplitude in REAPER and then used a sound level meter (CEM Instruments, model DT-85A) to normalize the amplitude of all playbacks to 85 dB at a distance of 1 m from the playback speakers to standardize the strength of the stimulus. Using a single speaker with multiple tracks raises the criticism that the simulation of multiple individuals could be confounded with an increase in signal frequency given by a single individual. To address this potential confound, we panned each track to emit different proportions of the recording from the left and right speakers of a dual speaker system. Speakers were placed 5 m apart, allowing us to simulate multiple individuals vocalizing from different locations and more accurately approximate the spatial arrangement of birds at a swarm. We used an Edirol recorder (model R-05, Roland Corporation) to broadcast playbacks and a second Edirol recorder attached to a tripod set at a height of 1.5 m to create an auditory log for later verification of species' identities. For each trial, we recorded the time of day to control for temporal effects on bird activity (e.g. foraging or vocal behaviour).

(e) Quantifying responses to playbacks

We measured responses of eavesdropping birds to playbacks following protocols described in Martínez *et al.* [20]. Briefly, we conducted unlimited distance point-counts [34] during a 10 min pre-trial (baseline), a 10 min trial (stimulus where vocalizations were broadcast) and a 10 min post-trial (to increase detection probability) to sample individual birds' responses to playbacks. Throughout each 30 min experiment, we spoke into a voice recorder (VN-701PC, Olympus) and kept a verbal log of all individuals that we saw or heard, and their distance and direction from the playback speakers to monitor their movements in real time. We estimated distance to the speakers based on preliminary trials in which we ground-truthed distances to vocalizing birds using a tape measure. Generally, individual birds that we detected in a particular direction retained that spatial orientation relative to the playback speakers throughout the experiment, allowing us to reliably distinguish different individuals of the same species. We defined a positive response to playbacks as individuals of ant-following species that approached within 15 m (the maximum distance at which birds are still considered part of a flock [35]) of the playback speakers during the stimulus or post-stimulus trial period. We are confident that our criteria for a positive response are valid, as responding individuals often stayed for several minutes in the vicinity of the speakers, vocalizing and apparently searching for an ant swarm.

(f) Statistical analysis

We used Bayesian generalized linear mixed models (GLMMs) to estimate recruitment of eavesdropping birds to simulated swarms at the island and mainland sites. Although there was substantial overlap in the island and mainland bird communities, with many shared species, the island community has lost a variety of resident bird species that are still currently present on the mainland. To control for these community-level differences in the pool of species available to respond to playbacks, we used a proportional metric that was site-specific and allowed us to compare the total number of responding individuals relative to the total number of individuals available to respond. Our response variable was the proportion of total individuals of all species that responded (i.e. came within less than or equal to 15 m of the speakers) relative to the total number of individuals detected at all distances in each 30 min trial.

We ran separate models for island and mainland sites. Because we were primarily interested in comparing responses to obligate playbacks with responses to control playbacks within sites. Therefore, although we collected data at the island and mainland sites in different years, we did not need to take sampling year into consideration in our statistical models. We found no significant differences in recruitment to small and large flock sizes for any of the three playback types at either site (all $p > 0.05$). Therefore, our final models included playback type as the sole fixed effect and calendar day (day since start of year) and trial start time as random effects in each model. For each model's covariance matrix of the two random effects and the residuals, we specified $V = 1$ and $\nu = 0.002$ as weak priors.

Each model was run for 2 000 000 MCMC iterations, with a 200 000 burn-in and a thinning interval of 1000. These settings yielded effective sample sizes greater than 1370 and MCMC chains with no observable autocorrelation. We visually inspected final trace plots and found good mixing properties. To ensure model convergence and repeatability, we ran each model two additional times to obtain three model runs. We calculated the Gelman–Rubin statistic [36], which uses a potential scale reduction factor (PSR) to compare within and between chain variance between replicate models. For mainland and island models, PSR for the sole predictor was 1.00–1.01 (less than 1.1 indicates model convergence). We randomly selected one replicate model for prediction, plotting and inference. We reran this model with

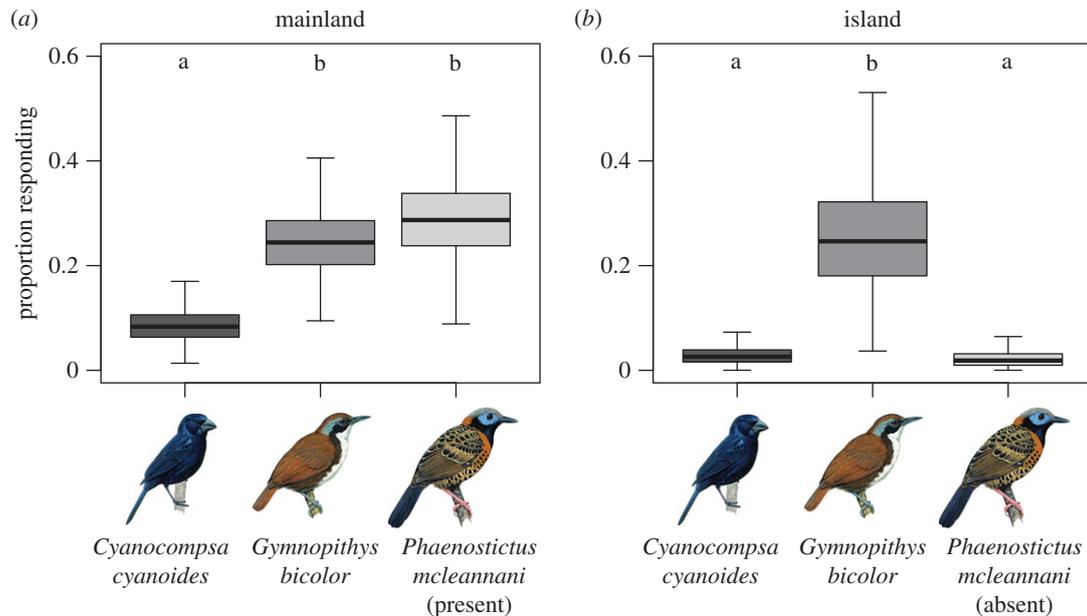


Figure 1. Proportion of ant-following bird species responding to the three different playback types: negative control (non-follower), *C. cyanoides*; positive control (obligate present), *G. bicolor*; obligate absent, *P. mcleannani*. (a) Mainland site; (b) island site. Letters indicate significant differences between treatment types within each site ($p_{\text{MCMC}} \leq 0.05$). Bird images reproduced with permission from Lynx Edicions [38].

an altered factor reference level to obtain estimates of all pairwise differences between dependency levels ($p_{\text{MCMC}} < 0.05$). Effects are presented as posterior mean (PM), 95% credible interval (lower and upper CI) and p_{MCMC} (the probability that the posterior distribution crosses zero). Bayesian GLMMs were implemented using the *MCMCglmm* package [37] within the R programming environment (v. 3.2.4).

3. Results

At the mainland site where the obligate ant follower *P. mcleannani* is still present, recruitment to playbacks of *P. mcleannani* was significantly higher (predicted proportion = 28.6%, 15.2–45.6% CI) than recruitment to negative control *C. cyanoides* (non-follower) playbacks (predicted proportion = 8.2%, 3.7–17.2% CI; $p_{\text{MCMC}} = 0.016$; figure 1a). Recruitment to playbacks of the positive control (the other obligate ant follower *G. bicolor*) was similar to that of *P. mcleannani* ($p_{\text{MCMC}} = 0.654$) and was also significantly higher than recruitment to negative control playbacks (predicted proportion = 23.9%, 13.4–37.3% CI; $p_{\text{MCMC}} = 0.015$; figure 1a). Thus, ant-following birds on the mainland recognized and recruited to vocalizations of the two present obligate species.

By contrast, we found strong evidence that island ant followers did not recognize or recruit to vocalizations of the locally extinct *P. mcleannani*, which has been absent from the island since the 1970s. Recruitment to playbacks of *P. mcleannani* on the island was very low (predicted proportion = 1.7%, 0.2–8.0% CI) and not significantly different from recruitment to the negative control *C. cyanoides* (non-follower) playback (predicted proportion = 2.4%, 0.5–7.5% CI; $p_{\text{MCMC}} = 0.693$; figure 1b). By contrast, we did find evidence of recruitment in response to *G. bicolor*, the obligate ant follower still present on the island. Recruitment to playbacks of *G. bicolor* was significantly higher than recruitment to the negative control playback (predicted proportion = 24.5%, 9.5–53.1% CI; $p_{\text{MCMC}} = 0.001$; figure 1b). Overall, the ant-following birds exhibited strong responses to playbacks of obligate species present at each site. However,

island ant followers did not respond to playbacks of the locally extinct *P. mcleannani*.

4. Discussion

Our comparative study provides convincing evidence that, in the case of ant-following birds, heterospecific eavesdropping is a learned behaviour acquired from past ecological experience with obligate ant followers. We found that the island ant followers did not recruit to playbacks of the absent obligate ant follower (*P. mcleannani*), but they did recruit to playbacks of the still present obligate ant follower (*G. bicolor*). Furthermore, we found that on the mainland, where both *P. mcleannani* and *G. bicolor* are present, ant followers recruited to playbacks of both obligate species. Taken together, these results suggest that ant-following birds recognize and recruit to ecologically relevant signals (i.e. vocalizations of obligate species present at each field site) indicating the presence of an ant swarm. If natural selection had resulted in innate heterospecific signal recognition, then island ant followers should have been able to recognize and recruit to vocalizations of the locally extinct *P. mcleannani*. However, the current island avifauna appears to have lost the ability to recognize *P. mcleannani* as an obligate ant follower after approximately eight generations of being absent [27]. Our results strongly suggest that eavesdropping birds learn to associate the vocalizations of particular species with the presence of ant swarms and do not innately recognize heterospecific signals.

Foraging at army ant swarms probably increases individual fitness because (i) it is a highly profitable food resource and (ii) foraging in groups often reduces risk of predation [39–41]. Given that obligate ant followers have coevolved to depend exclusively on army ants for food [21], their vocalizations are a highly reliable cue indicating the presence of this profitable resource [18–20,23]. Therefore, we speculated that these putative fitness benefits might select for innate signal recognition of obligate ant followers. Instead, we found that birds learn by association from ecological experience. Our

results are consistent with the preponderance of evidence in the literature demonstrating that heterospecific eavesdropping seems to be a learned behaviour [3,12,14,42–44]. Innate recognition of heterospecific signals has rarely been documented in birds (but see [9,10,17,45]), although there is some evidence of innate recognition of predator signals in other vertebrates [46–48]. Nevertheless, the fitness costs of being depredated are much more likely to be higher than the costs of not recognizing a beneficial food resource, and therefore species may be more likely to evolve innate responses to predators [46,49] than to food resources.

Evaluating whether a behaviour is learned or innate is a challenging endeavour because information about individuals' past ecological experiences is necessary to rule out learning as the underlying mechanism. We took advantage of the isolation of BCI from the mainland of Panama and the subsequent local extinction of an obligate ant follower to infer the past ecological history of the island avifauna. An alternative hypothesis for the differential responses we have documented is that, either prior to or because of the isolation of the island site, island and mainland birds have accumulated genetic differences at the population level that have influenced eavesdropping behaviour. It is highly unlikely that these genetic differences were present prior to the island's isolation because the island was connected to the mainland via contiguous forest and their communities were nearly identical [27]. Furthermore, we consider it unlikely that island birds have lost their ability to recognize *P. mcleanmani* vocalizations in the span of only approximately eight generations because the island's isolation. Finally, if genetic differences were responsible for differential responses to *P. mcleanmani* vocalizations between island and mainland populations, the same differential responses would be expected for *G. bicolor*, yet we found no difference in island and mainland responses to *G. bicolor* vocalizations. To determine if there were genetic differences between island and mainland bird populations responsible for differential responses to playbacks would require experimentally manipulating a

community and or conducting a controlled breeding experiment to infer causation, which is simply not tractable for this system. In addition, there is some evidence from another antbird species (black-crowned antshrike—*Thamnophilus atrinucha*) that exists at both sites that genetic differences between island and mainland populations are minimal (D. Maddox and C.E.T. 2014, unpublished data). Therefore, although it is not possible to exclude the alternative hypothesis of population genetic differences, our results strongly suggest that the mechanism of heterospecific signal recognition in this system is learning by past ecological experience. Whether ant-following birds learn through cultural transmission [50] or through individual experience [51] is an open question that will require further testing.

Ethics. This research was conducted under the auspices of the Smithsonian Tropical Research Institution (STRI). Research permits were provided by the Administración Nacional del Ambiente (ANAM). All protocols were approved by the STRI Institutional Animal Care and Use Committee (no. 2013-0101-2016). All research was approved by the Smithsonian Tropical Research Institute Institutional Animal Care and Use Committee under permit no. 2015-0102-2018.

Data accessibility. Supporting data can be found in the electronic supplementary material and at Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.k17g2>) [52].

Authors' contributions. H.S.P., A.E.M., J.P.K., J.M.T. and C.E.T. designed the research; A.E.M., J.P.K. and C.E.T. obtained and edited the playbacks; H.S.P. and A.E.M. collected the data; J.P.K. and C.E.T. analysed the data; H.S.P., A.E.M., J.P.K., J.M.T. and C.E.T. wrote the paper.

Competing interests. The authors declare no competing interests.

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