Breeding density, not life history, predicts interpopulation differences in territorial aggression in a passerine bird

Jongmin Yoon [a,1], T. Scott Sillett [b], Scott A. Morrison [c], Cameron K. Ghalambor [a,*]

[a] Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, U.S.A.
[b] Smithsonian Conservation Biology Institute, Migratory Bird Center, National Zoological Park, Washington, D.C., U.S.A.
[c] The Nature Conservancy, San Francisco, CA, U.S.A.

Interpopulation variation in territorial aggression can reflect differences in life history or competitive environments. Life history theory predicts that males with more opportunities for future reproduction should avoid risk-taking behaviour to minimize the cost of current reproduction, whereas competitive environments should favour higher aggression to defend limited resources. Additionally, male aggression can be modulated by familiarity with competitors to be either lower (dear enemies) or higher (nasty neighbours) towards neighbours. We conducted a territory intrusion experiment using neighbour–stranger songs to examine how territorial aggression differed in two populations of orange-crowned warblers, *Oreothlypis celata*, breeding in California and Alaska. The California population breeds at very high densities and has a higher annual survival relative to the Alaska population, which breeds at significantly lower densities and has a lower annual survival rate. We found that California males showed higher amounts of territorial aggression in response to simulated territory intrusions than did Alaska males, supporting the hypothesis that competitive environments, as indicated by breeding density, rather than life history, shape geographical variation in levels of aggression. Both populations discriminated between song stimuli of neighbours and strangers, but California males responded more strongly towards neighbours, whereas Alaska males responded more strongly towards strangers. We discuss these results in light of the mechanisms for overall aggression and neighbour–stranger discrimination.

© 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Male territorial aggression is thought to be an adaptive response to competitors as it can increase access to food resources, breeding space and mates (Brown 1964, 1969). However, territorial aggression also involves fitness costs because overly aggressive individuals can experience increased risk of physical injuries that reduce survival and limit parental care (Wingfield et al. 1990, 2001). Males should not increase territorial aggression beyond the point where fitness costs exceed benefits (Brown 1964, 1969), yet few studies have tested alternative hypotheses for intra- or interspecific variation in territorial aggression. Life history theory predicts that territorial males in species or populations that show comparatively low adult survival and high fecundity should invest more time and energy into current reproductive effort compared with males in populations with comparatively high survival and low fecundity

(Stearns 1992; Ricklefs & Wikelski 2002; Roff 2002). Indeed, elevated aggression towards conspecifics and boldness towards predators are forms of risk-taking behaviours that are expected to be more likely in species or populations with a relatively low probability of surviving to breed in the future (i.e. low residual reproductive value; Clark 1994; Ghalambor & Martin 2001; Wolf et al. 2007). Alternatively, competitive environments, such as those with high conspecific densities, have been thought to favour elevated territoriality to acquire and defend resources (Brown 1964; Grant 1993; Stamps 1994).

Comparative studies of populations that differ in breeding densities and life histories allow for tests of contrasting predictions about the causes of variation in male territorial aggression. For example, long-distance migrants that breed at high latitudes typically have large clutch sizes and relatively high annual adult mortality (Martin et al. 2000; Ghalambor & Martin 2001; Sillett & Holmes 2002; Martin 2004), and they breed in habitats that are typically characterized as having low density and relatively abundant food (Ashmole 1963; Cody 1966; MacArthur 1972; Ricklefs 1980; Levey & Stiles 1992). Thus, life history theory would predict that long-distance migrants would be more aggressive in territorial

* Correspondence: C. K. Ghalambor, Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, U.S.A.
E-mail address: cameron.ghalambor@colostate.edu (C. K. Ghalambor).
[1] J. Yoon is now at the Korea Institute of Oriental White Stork Reintroduction Research Center, Department of Biology Education, Korea National University of Education, Cheongwon, Chungbuk 363-791, South Korea.

defence because of their 'fast' life histories (Ricklefs & Wikelski 2002), whereas resource competition theory predicts that they would be less aggressive because food abundance is high and conspecific density is low (Ashmole 1963; Cody 1966; MacArthur 1972; Ricklefs 1980). Despite these contrasting predictions, few studies to date have focused on testing the factors driving interpopulation variation in male aggressive behaviour (see also Akçay et al. 2009).

The level of territorial aggression in a population can also be mediated by individual recognition of competitors as a precondition for adaptive moderation of aggressiveness (Kroodsma & Miller 1996). For example, the 'dear enemy' hypothesis predicts that individuals should be less aggressive towards familiar individuals of a known threat to avoid the costs associated with repetitive territorial contests (Fisher 1954; Trivers 1971; Ydenberg et al. 1988). Support for the dear enemy hypothesis has been found in studies of many taxa, including insects (Heinze et al. 1996), fish (Frostman & Sherman 2004), amphibians (Jaeger 1981), reptiles (Whiting 1999), birds (Eason & Hannon 1994) and mammals (Price et al. 1990). Reduced aggression towards familiar individuals can optimize time and energy expenditure for territory defence and maximize shared mutual benefits among neighbours (Wilson 1975). Conversely, the threat-level, or 'nasty neighbour', hypothesis predicts that selection should favour territorial owners that respond more aggressively towards neighbours (Temeles 1994; Müller & Manser 2007). Increased aggression towards familiar neighbours is thought to occur when such individuals represent a greater threat for food resources, space or mates compared to unfamiliar strangers (Temeles 1994; Müller & Manser 2007). However, territorial males may show both strategies for individual recognition as a conditional response to dynamic changes in population density or resource limitation: 'dear enemies' if being aggressive towards neighbours is too costly, or 'nasty neighbours' when resource sharing is not negotiable (Müller & Manser 2007; Briefer et al. 2008; Newey et al. 2008). Nevertheless, the factors shaping population differences in territorial responses towards neighbours versus strangers remain poorly understood.

We simulated territorial intrusions to examine (1) the factors that shape geographical variation in male aggression and (2) neighbour–stranger discrimination. We tested aggressive responses to playbacks of neighbour and stranger songs in two breeding populations of orange-crowned warblers, Oreothlypis celata (Parulidae) that differ in a measure of resource competition (i.e. population density) and life history: O. c. celata in Fairbanks, central Alaska (hereafter Alaska warblers), and O. c. sordida on Santa Catalina Island, off the coast of southern California (hereafter California warblers). These two populations have contrasting life histories. The Alaska population has a 'faster' life history with a low annual survival probability (mean $\pm$ SE = 0.40 $\pm$ 0.16 for males) and large clutch sizes (5–7 eggs), compared with the California population (annual male survival probability, 0.75 $\pm$ 0.02; clutch size, 2–4 eggs; Horton et al. 2010; C. K. Ghalambor & T. S. Sillett, unpublished data). The Alaska population also breeds at a significantly lower density and presumably experiences a less competitive breeding environment than the California population (see Results). These differences in life history and breeding density yield contrasting predictions about levels of male aggression in our study system. Life history theory predicts that California males have relatively more opportunities for future reproduction and should show relatively lower aggression towards conspecifics during territory defence, compared to Alaska males. In contrast, resource competition theory predicts that high conspecific breeding density should favour elevated aggression towards neighbours in California males relative to Alaska males. Higher breeding densities and frequent territorial contests could favour reduced aggression towards neighbours (dear enemies) in California, but could also result in elevated aggression towards neighbours (nasty neighbours) if they pose a greater threat than strangers or unfamiliar individuals.

METHODS

Study Sites and Populations

The orange-crowned warbler is a widespread, socially monogamous breeder in temperate forest and scrub habitats in western and northern North America (Sogge et al. 1994). We studied the Alaska population on an 88 ha plot near Fairbanks, Alaska (64°47′41″N, 147°53′45″W) and the California population on a 14 ha plot on Santa Catalina Island, California (33°20′56″N, 118°26′59″W) during the 2007 and 2008 breeding seasons (late February to mid-May in California; mid-May to early July in Alaska). The Alaska study site was dominated by spruce (Picea), birch (Betula) and willow (Salix) habitat, whereas the California site was characterized by oak (Quercus) and associated chaparral habitat. Males established territories used for both breeding and foraging in late February in California and in mid-May in Alaska. Territorial establishment in both populations was characterized by frequent male singing and territorial fights among neighbouring males but was less synchronized in California (occurring over approximately 1 month) than in Alaska (occurring over approximately 2 weeks; J. Yoon, personal observation). Nest predation (and hence renesting) was more frequent in the California population than in the Alaska population (mean $\pm$ SE nest survival probability: 0.20 $\pm$ 0.01 in Alaska versus 0.40 $\pm$ 0.01 in California; Horton et al. 2010). Overall, these differences corresponded to a longer breeding season in California (100–120 days) than in Alaska (50–60 days; Horton et al. 2010).

Breeding Density Measures

Warblers at both study sites were colour banded, and their nesting success was monitored to facilitate the collection of territory information and breeding density. We captured adults with mist nets and banded them with a unique combination of three coloured leg bands and a numbered aluminium U.S. Geological Survey band to identify each individual. Individuals' sex and age were determined based on morphological and plumage characters (Pyle 1997). All warbler territories were mapped by observing movements and boundary disputes of banded males and females throughout the breeding season. To facilitate individual identification and territory mapping (during 0400–1200 hours in Alaska, and 0600–1200 hours in California), we delineated plots into 25 $\times$ 25 m grids with flagging tape, and waypoints of all grid intersections were incorporated into ArcGIS version 9.1 (ESRI Inc., Redlands, CA, U.S.A.). We marked the daily locations of individual warblers on field sheets printed with the plot grids overlaid onto aerial photographs and with global positioning system (GPS) waypoints. Final territory boundaries were determined by a minimum convex polygon (Ford & Myers 1981) in ArcGIS. Breeding density was calculated as the number of territories divided by the total area of each study plot. When territories partially overlapped with the fixed extent of the study site, the proportion of territory size (e.g. less than 1.0) extending onto the plot was used. We found and monitored nests of 30–40 warbler pairs per site each breeding season and checked them every 2–3 days to confirm fledging or failure. Warbler pairs were followed intensively after nest failure to locate new nests or to confirm the cessation of breeding for that season.

Male Singing Behaviour

We recorded the singing behaviour (singing versus nonsinging) of territorial males during three breeding stages: preincubation, incubation and nestling periods. Territories were randomly selected for visits to quantify singing behaviour. These observations were conducted for 2 min in March–May in California (0600–1200 hours) and May–June in Alaska (0400–1200 hours), and each observation for a territory did not exceed more than one observation per day.

Playback Stimuli

We recorded songs from 30–40 focal males per study site to obtain a catalogue of song stimuli for use in our simulated territorial intrusion experiments (hereafter STIs). Songs were recorded in March in California (0700–1100 hours) and in May in Alaska (0400–0800 hours) with a parabolic microphone (P–650, Dan Gibson Electronics) and a MiniDisk recorder (MZ–NH1, Sony Inc.) at a distance of 5–10 m from singing warblers. We saved songs in an uncompressed format (PCM format, 16 bits at 44.1 kHz) to minimize loss of high-frequency sounds and transferred them to Waveform Audio File Format (.wav) using a digital sound program (Sonic Stage version 4.0, Sony Inc.). While some high-frequency sounds may have been lost during this process, the same approach was used in both study sites.

Males in both populations sang a repertoire with a repeat of a single song type, which was stable within and between years (J. Yoon, personal observation). We therefore expected that playbacks generated from the relatively simple song types of our orange-crowned warbler populations were less likely to hinder individual recognition (neighbours versus strangers), compared to species with larger repertoires (Falls 1982). Songs of each focal male were assembled in the program Syrinx (John Burt, www.syrinxpc.com, Seattle, WA, U.S.A.) to create a standardized 5 min song stimulus. The song stimulus contained a repeat of the same song type with an 8 s break between each song, resulting in a song rate of six songs/min for both populations. We also used the amplitude and background noise filter functions in Syrinx to equalize playback stimuli (Mennill & Ratcliffe 2000).

Playback Methods

We performed STI sessions using neighbour and stranger song playbacks to males in each population and defined males adjacent to a target territory as 'neighbours' and males more than two territories away from the target male as 'strangers' (mean ± SE distance between target and stranger male territories: Alaska: 504.7 ± 37.2 m, $N = 25$; California: 296.4 ± 31.0 m, $N = 24$). Higher conspecific densities and smaller territory sizes yielded shorter distances between target males and strangers in California (33.3 ± 0.7 m) compared to Alaska (92.6 ± 3.5 m). However, our preliminary test found no significant relationship between aggression level and distance to stranger males in either the Alaska (Pearson correlation: $r_{23} = 0.16$, $P = 0.44$) or California ($r_{22} = −0.19$, $P = 0.38$) populations. Thus, we excluded a proximity covariate such as distance between the target and stranger territory for song stimuli in our final analyses. Nevertheless, we used our detailed movement data and territory maps to ensure that no stranger was observed near the territory of the focal male. The stimulus consisted of a loudspeaker and a male *O. celata* taxidermic mount that we placed in the approximate centre of a target territory, allowing for sufficient space for target males to respond freely (e.g. aggressive flights in the range of 0–5 m from the stimulus) and a perch for the male to stay within a range of 0–2 m. We used an identical portable speaker (frequency response: 150 Hz–20 kHz; Creative Technology Ltd, Singapore) connected to an identical MP3 player (SanDisk Corp., Milpitas, CA, U.S.A.) with the same volume level to standardize playback stimuli for both populations. The observer (J. Yoon) was concealed 5 m from the stimulus to record behavioural responses of the target male, and he waited 5 min after setting up the speaker and mount to start the song playback to minimize any modification of the target male's behaviour. We conducted two STI sessions per male: one session using a neighbour song and the other using a stranger song. Two STI sessions per male were at least 24 h apart, and the order of neighbour and stranger presentations was randomized. The use of randomly selected songs of neighbours and strangers was designed to avoid pseudoreplication (McGregor et al. 1992).

Response Measures

We recorded a suite of vocal and physical responses during STIs. Two vocal response variables included (1) the number of calls (i.e. a variable number of chip notes as a form of alarm calls) and (2) the number of songs. Martin & Martin (2001) measured only song-related responses (e.g. number of songs and song overlap) as a vocal response during STIs in the same species, but we included nonsong vocalizations because we frequently observed both song and calls during territorial disputes under natural and experimental conditions. Four flight response variables were also measured. These responses included two proximity measurements, the number of flights observed within 0–2 m from the stimulus (hereafter proximate flight) and the number of flights observed within 2–5 m (hereafter distant flight), and two time measurements, the latency to respond to the stimulus (5 min minus the time it took the male to approach within 0–5 m of the stimulus; see McGregor 1992; hereafter latency) and the time that the male stayed within 0–2 m of the stimulus. If males did not respond to the playback within 5 min, then a latency of 5 min was attributed to such males as a response time. To control for stage of reproduction, we conducted STIs during the incubation period of the focal male's mate (only females incubate in this species), which typically occurred in April for the California population and in June for the Alaska population. An extreme drought occurred on Santa Catalina Island in 2007 and all breeding attempts failed (Langin et al. 2009). However, STIs were still conducted because males were paired with females and defended their territories until the beginning of May, as would happen in a typical year (J. Yoon, personal observation).

Statistical Methods

We used a two-sample *t* test to compare the means of breeding densities between the two populations and a sequence of statistical methods to characterize male aggressiveness and to analyse the STI data. We analysed singing and associated aggressive behaviours in relation to breeding stage, site (Alaska versus California) and the two-way interaction using a general linear mixed model with restricted maximum likelihood (REML). Individual male band number was included as a random effect. Fisher's least significant difference (LSD) was used to examine significant interaction effects. Because many of these response variables were correlated with each other, we then used a principal components analysis (PCA) to generate a composite aggression score from the six correlated responses (i.e. number of calls and songs, proximate and distant flights, latency to respond and time spent near stimulus) for each focal male (McGregor 1992). We analysed the PCA-derived score with a general linear mixed model fit. Fixed predictor variables were site, stimulus type (neighbour versus stranger songs), year (2007 versus 2008), playback order (first versus second trials), distance between target and stranger territories (m), and all

two-way interactions. Our initial analyses revealed no significant effects of year or playback order, and no interactions involving these variables ($P > 0.50$); therefore, we omitted these terms from final analyses presented here. All statistical analyses were performed in SPSS version 13.0 (SPSS Inc., Chicago, IL, U.S.A.). We did not need to transform any variables to meet model assumptions. Behavioural responses are presented as means $\pm$ 1 SE.

Ethical Note

The present study involved short-term presentations of song stimuli to study subjects. The observed level of aggressive behaviour was close to natural interactions between territorial males and did not have any observable, lasting effects after playbacks ended. All research was conducted under ASAB/ABS guidelines and approved by the Institutional Animal Care and Use Committee of Colorado State University (08−342A−01).
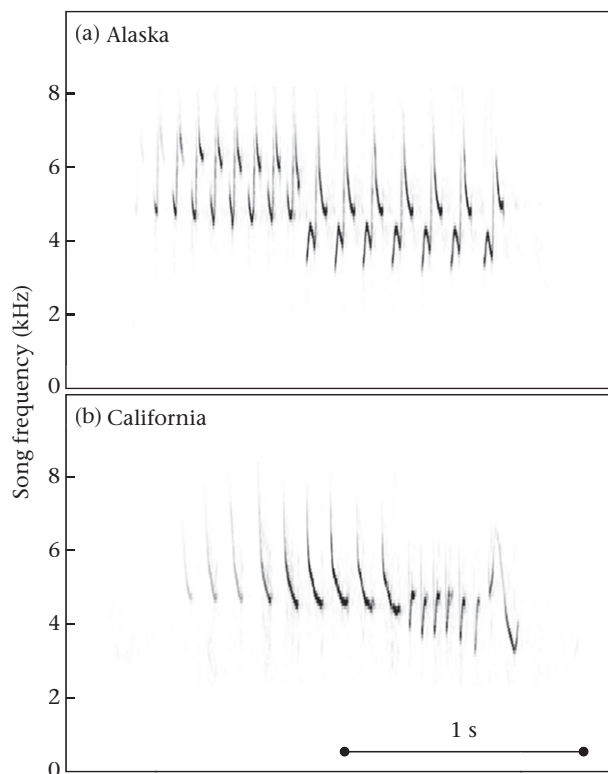
RESULTS

Breeding Densities

Warbler breeding density was significantly lower in the Alaska population than in the California population (two-sample t test: $t_2 = -5.30$, $P = 0.03$). Mean breeding density was 0.48 ± 0.02 territories/ha in Alaska ($N = 2$ years) and 4.11 ± 0.97 territories/ha in California ($N = 2$ years).

Male Singing Behaviour

Males sang slightly different songs between populations: Alaska males sang a thin, fast trill, and the California males sang a slower, lower-pitched trill (Fig. 1). While Alaska males sang more frequently throughout the breeding season than California males (52% versus 25%, respectively; mixed model: site: $F_{1,305} = 8.03$, $P < 0.01$; Fig. 2), the proportion of singing males significantly decreased throughout the breeding stages in both populations (stage: $F_{2,530} = 8.05$, $P < 0.001$; site $\times$ stage: $F_{2,530} = 0.25$, $P = 0.78$; Fig. 2).

Male Aggressive Behaviours

Alaska and California males had different patterns of behavioural response to our STI experiment regardless of the stimuli (Fig. 3). The number of calls given in response to STI was higher in California than in Alaska, whereas the number of songs in response to STI was higher in Alaska than in California (mixed model: site: $F_{1,49} = 9.44$, $P < 0.01$; type: $F_{1,159} = 82.80$, $P < 0.001$; site $\times$ type: $F_{1,159} = 36.78$, $P < 0.001$; Fig. 3a). The number of proximate flights did not differ between the two populations, but the number of distant flights was higher in California (site: $F_{1,51} = 4.59$, $P = 0.04$; type: $F_{1,161} = 2.75$, $P = 0.10$; site $\times$ type: $F_{1,161} = 6.39$, $P = 0.01$; Fig. 3b). California males responded more quickly (i.e. shorter latencies to respond) and stayed near the stimulus longer than did Alaska males (site: $F_{1,51} = 16.26$, $P < 0.001$; type: $F_{1,161} = 136.32$, $P < 0.001$; site $\times$ type: $F_{1,161} = 0.90$, $P = 0.35$; Fig. 3c).

The multivariate behavioural responses to STI were reduced to a single principal component (PC1) that accounted for 40.6% of the total variance in male aggressive behaviour (eigenvalue = 2.43) and represented a gradient from relatively less aggressive to more aggressive responses to the STI experiment (Table 1). No other subsequent PC scores had eigenvalues ≥ 1 and were thus excluded from subsequent analyses. PC1 was positively correlated with the number of calls, number of proximate flights, number of distant flights, latency to respond and time spent near the stimulus in both populations, but the number of songs was negatively correlated with PC1 in Alaska and uncorrelated in California (Table 1).
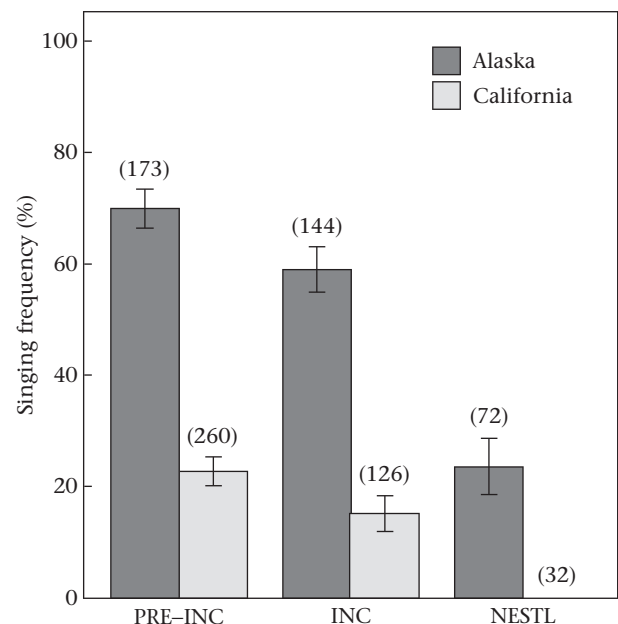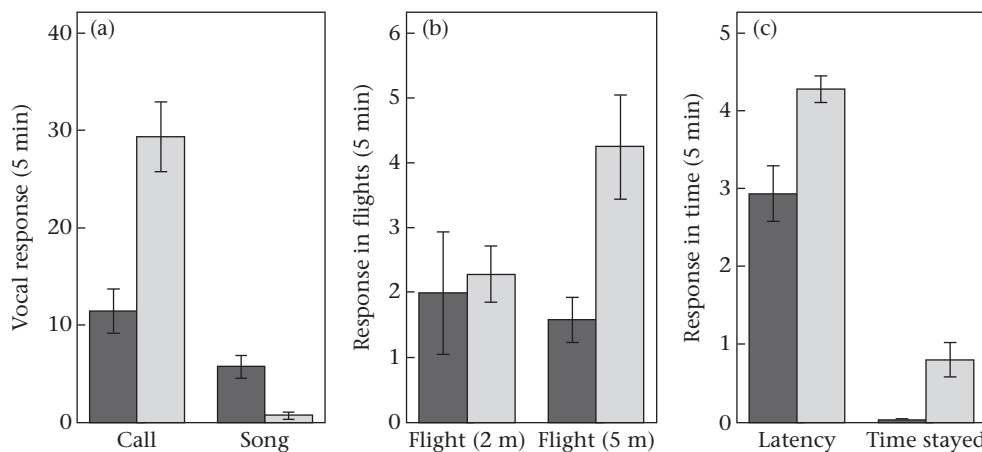

Figure 1. Song spectrographs of male orange-crowned warblers breeding (a) in Fairbanks, Alaska and (b) on Santa Catalina Island, California, U.S.A.

Figure 2. Frequency of singing activity in breeding orange-crowned warblers in Fairbanks, Alaska, and on Santa Catalina Island, California, U.S.A. Bars represent mean $\pm$ SE frequencies of song output (singing = 1, nonsinging = 0) in relation to breeding stage: preincubation (PRE-INC), incubation (INC) and nestling (NESTL) periods. Observations for randomly selected males for 2 min territory visits (during 0400−1200 hours in Alaska, and during 0600−1200 hours in California) were not recorded more than two times per day.

Figure 3. Six behavioural measures of male aggression in breeding orange-crowned warblers in Fairbanks, Alaska (dark grey bars; $N = 27$), and on Santa Catalina Island, California (light grey bars; $N = 27$), U.S.A., in response to territorial intrusions simulated by song playbacks and a taxidermy mount: (a) numbers of calls and songs; (b) number of proximate (0–2 m from the stimulus) and distant (2–5 m from the stimulus) flights; (c) rescaled latency to respond (i.e. 5 min minus the time that it took a male to approach within 0–5 m of the stimulus) and time spent within 0–2 m of the stimulus ('time stayed'). Bars represent means ± SE of averaged behaviours in response to neighbour–stranger song stimuli.

Our mixed model ANOVA revealed that male aggression level and response to neighbours and strangers differed between Alaska and California males (Fig. 4). Overall male aggression was higher in California than in Alaska, but the relationship between male aggression and song stimulus type differed between warbler populations (mixed model: site: $F_{1,52} = 22.41$, $P < 0.001$; stimulus: $F_{1,52} = 0.02$, $P = 0.90$; stimulus x site: $F_{1,52} = 25.94$, $P < 0.001$). Specifically, Alaska males responded significantly less aggressively towards neighbour songs than they did towards stranger songs (LSD: $F_{1,26} = 11.53$, $P < 0.01$; see Fig. 4). In contrast, California males responded more aggressively towards neighbour songs than they did towards stranger songs (LSD: $F_{1,26} = 14.63$, $P = 0.001$; Fig. 4).
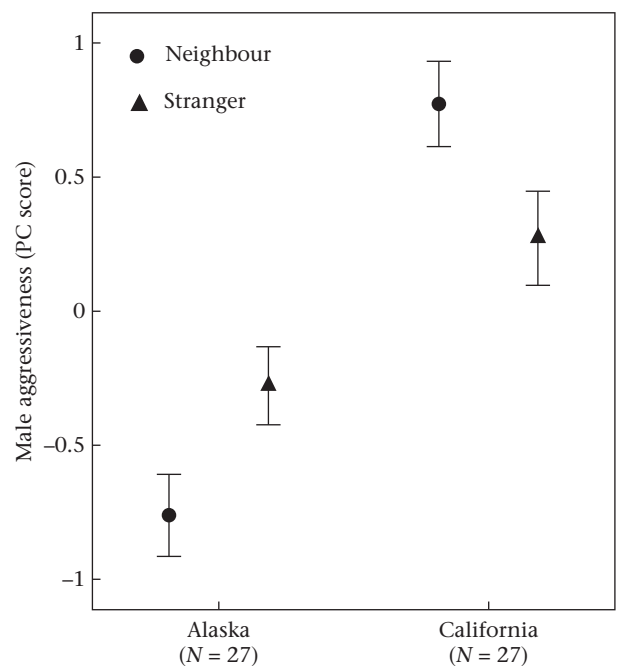
DISCUSSION

We hypothesized that interpopulation patterns of male aggression in our study would be shaped either by life history or resource competition as reflected by conspecific density. Our results support the predictions from the resource competition hypothesis. We found that while both populations show a seasonal decrease in singing activity (Fig. 2), when controlling for breeding stage, Alaska males showed reduced overall aggression towards conspecifics compared with California males (Figs 3, 4; see also Table 1). Given the significantly higher breeding density and annual adult survival in California compared to Alaska, these results are opposite to predictions from life history theory but consistent with predictions based on resource competition. Indeed, California

males responded to STI by performing more frequent call notes and flights, responding more quickly to the stimulus and spending more time near the stimulus relative to Alaska males (Figs 3, 4). Goss-Custard et al. (1984) reported a similar pattern of aggression in European oystercatchers, *Haematopus ostralegus*; aggressiveness increased between individuals at higher competitor densities but disappeared at low densities. The differences in male aggressive behaviours that we document here are also consistent with variation in male testosterone levels documented in the same populations: testosterone levels of males stay high throughout the breeding season in California and decline over the breeding season in Alaska (Horton et al. 2010). Elevated testosterone levels are associated with high population density in other passerine species

Table 1
Pearson correlation coefficients between six aggressive behaviours and PC1 (see Methods) for male orange-crowned warblers breeding in Fairbanks, Alaska, and on Santa Catalina Island, California, U.S.A.

Response type	Alaska		California	
	r_{52}	P	r_{52}	P
No. of calls	**0.66**	<0.001	**0.66**	<0.001
No. of songs	−**0.44**	0.001	−0.16	0.259
No. of proximate flights (0–2 m)	**0.59**	<0.001	**0.71**	<0.001
No. of distance flights (2–5 m)	**0.48**	<0.001	**0.71**	<0.001
Latency to respond*	**0.83**	<0.001	**0.73**	<0.001
Time spent within 0–2 m	**0.35**	0.009	**0.63**	<0.001

* Latency to respond (5 min minus the time that the male took to approach within 0–5 m of the stimulus). Significant values are shown in bold.

Figure 4. Patterns of aggression level and response to neighbours versus strangers of male orange-crowned warblers breeding in Fairbanks, Alaska, and on Santa Catalina Island, California, U.S.A., in response to neighbour and stranger song playbacks. Error bars represent ±1 SE of the first PC score.

(Ball & Wingfield 1987; Wingfield & Hahn 1994). Ultimately, more comparative and experimental studies of populations that differ in breeding density are necessary to establish the generality of these results.

Nasty Neighbours in California Males

California males responded more aggressively towards songs of neighbours versus strangers (i.e. nasty neighbours; Temeles 1994), suggesting that neighbours are perceived as the greater threat. Warbler territory density was approximately 10 times higher in California than in Alaska, and little to no buffer existed between most warbler territories in California, whereas territories in Alaska were often separated by unoccupied space. Conspecific neighbours share a common interest in resource use so that intense competition among neighbours should occur through recognizing one another as a threat (Temeles 1994). Thus, increased competition for space might underlie neighbour–stranger discrimination. Such directed aggression may occur over food or space (Temeles 1990; Dunn & Messier 1999; Müller & Manser 2007), or over access to mates (Brunton et al. 2008). Indeed, greater asynchronous breeding, higher renesting rates due to nest predation, and an overall longer breeding season in California could also explain higher aggression towards neighbours if such conditions provide more opportunities for extrapair matings (Birkhead & Biggins 1987; Birkhead & Møller 1992). The competitive, highly dense environment in our study site on Santa Catalina Island might also favour breeding males that call more frequently, rather than sing at higher rates, and are more likely to display a physical response to intruders, compared to breeding males in Alaska (Figs 2, 3). Further research is necessary to reveal how territorial males perceive neighbours as a greater threat to their paternity compared with strangers.

Dear Enemies in Alaska Males

A higher tolerance against known neighbours is thought to minimize the frequency of costly interactions among territory holders (i.e. dear enemies; Fisher 1954). We found that Alaska males responded less aggressively towards the songs of neighbours than towards strangers. While such results have been frequently documented in other studies, why such neighbour–stranger discrimination occurs in Alaska is less clear. Breeding density in Alaska is similar to that of other continental parulid populations (e.g. Porneluzi & Faaborg 1999; Sillett et al. 2004), and while territorial disputes are common early in the breeding season, they are uncommon compared to California. Yet, greater aggression towards strangers in Alaska suggests that the level of interaction among neighbours is sufficient to use a dear enemy strategy. It would be insightful to know the degree to which this dear enemy strategy is conditional, and whether the Alaska population would shift aggression towards neighbours under conditions of higher density and greater territorial contests. For example, male hooded warblers, Wilsonia citrina, showed increased territorial aggression towards neighbours after repeated intrusions along shared boundaries (Godard 1993), and male sand fiddler crabs, Uca pugilator, that initially showed a dear enemy response shifted towards greater aggression towards neighbours when the distance between burrows was experimentally reduced (Pratt & McLain 2006). Thus, behavioural responses within and between populations may not represent fixed strategies, but rather conditional ones that are plastic with respect to the local environment.

Relative Aggression and Neighbour–Stranger Recognition

Our results suggest that when male aggression increases, it does so under all contexts (Fig. 4). For example, if breeding density drives higher levels of overall aggression, it does so in response to both neighbour and stranger songs. Indeed, the maintenance of high levels of testosterone in males throughout the breeding season in California would suggest a mechanism that underlies high overall levels of aggression. Alternatively, strangers in the California population may represent a substantial threat that, while not as great as neighbours, still requires an aggressive response. One hypothesis that could explain such a relatively strong response to strangers in California is that unknown individuals could represent non-territorial floaters still searching for territories (Smith 1978; Zack & Stutchbury 1992). We suspect that floaters are more common and thus territory incursions from floaters are more frequent in California (see Langin et al. 2009), compared to Alaska. Confirmation of the generality of our findings, however, will require additional, comparative studies that examine how overall aggression and neighbour–stranger recognition are linked or decoupled in populations that differ in breeding density.

Acknowledgments

References

Akçay, Ç., Wood, W. E., Searcy, W. A., Templeton, C. N., Campbell, S. E. & Beecher, M. D. 2009. Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. Animal Behaviour, **78**, 97–102.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis, **103**, 458–473.

Ball, G. F. & Wingfield, J. C. 1987. Changes in plasma levels of sex steroids in relation to multiple broodness and nest site density in male starlings. Physiological Zoology, **60**, 191–199.

Birkhead, T. R. & Biggins, J. D. 1987. Reproductive synchrony and extra-pair copulation in birds. Ethology, **74**, 320–334.

Birkhead, T. R. & Møller, A. P. 1992. Sperm Competition in Birds: Evolutionary Causes and Consequences. London: Academic Press.

Briefer, E., Rybak, F. & Aubin, T. 2008. When to be a dear enemy: flexible acoustic relationships of neighbouring skylarks, Alauda arvensis. Animal Behaviour, **76**, 1319–1325.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin, **76**, 160–169.

Brown, J. L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. Wilson Bulletin, **81**, 293–329.

Brunton, D. H., Evans, B., Cope, T. & Ji, W. 2008. A test of the dear enemy hypothesis in female New Zealand bellbirds (Anthornis melanura): female neighbors as threats. Behavioral Ecology, **19**, 791–798.

Clark, C. W. 1994. Antipredator behavior and the asset-protection principle. Behavioral Ecology, **5**, 159–170.

Cody, M. L. 1966. A general theory of clutch size. Evolution, **20**, 174–184.

Dunn, R. & Messier, S. 1999. Evidence for the opposite of the dear enemy phenomenon in termites. Journal of Insect Behavior, **12**, 461–464.

Eason, P. & Hannon, S. J. 1994. New birds on the block: new neighbors increase defensive costs for territorial male willow ptarmigan. Behavioral Ecology and Sociobiology, **34**, 419–426.

Falls, J. B. 1982. Individual recognition by sound in birds. In: Acoustic Communication in Birds (Ed. by D. E. Kroodsma & E. H. Miller), pp. 237–273. New York: Academic Press.

Fisher, J. 1954. Evolution and bird sociality. In: Evolution as a Process (Ed. by J. Huxley, A. C. Hardy & E. B. Ford), pp. 71–83. London: Allen & Unwin.

Ford, R. G. & Myers, J. P. 1981. Evaluation and comparison of techniques for estimating home range and territory size. Studies in Avian Biology, **6**, 461–465.

Frostman, P. & Sherman, P. T. 2004. Behavioral response to familiar and unfamiliar neighbors in a territorial cichlid, Neolamprologus pulcher. Ichthyological Research, **51**, 283–285.

Ghalambor, C. K. & Martin, T. E. 2001. Fecundity–survival trade-offs and parental risk-taking in birds. *Science*, **292**, 494–497.

Godard, R. 1993. Tit for tat among neighboring hooded warblers. *Behavioral Ecology and Sociobiology*, **33**, 45–50.

Goss-Custard, J. D., Clarke, R. T. & Le V. Dit Durell, S. E. A. 1984. Rates of food intake and aggression of oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. *Journal of Animal Ecology*, **53**, 233–245.

Grant, J. W. A. 1993. Whether or not to defend? The influence of resource distribution. *Marine Behavior and Physiology*, **23**, 137–153.

Heinze, J., Foitzik, S., Hippert, A. & Hölldobler, B. 1996. Apparent dear-enemy phenomenon and environment-based recognition cues in the ant *Leptothorax nylanderi*. *Ethology*, **102**, 510–522.

Horton, B. M., Yoon, J., Ghalambor, C. K., Moore, I. T. & Sillett, T. S. 2010. Seasonal and population variation in male testosterone levels in breeding orange-crowned warblers (*Vermivora celata*). *General and Comparative Endocrinology*, **168**, 333–339.

Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. *American Naturalist*, **117**, 962–974.

Kroodsma, D. E. & Miller, E. H. 1996. *Ecology and Evolution of Acoustic Communication in Birds*. Ithaca, New York: Cornell University Press.

Langin, K. M., Sillett, T. S., Yoon, J., Sofaer, H. R., Morrison, S. A. & Ghalambor, C. K. 2009. Reproductive consequences of an extreme drought for orange-crowned warblers on Santa Catalina and Santa Cruz Islands. In: *Proceedings of the Seventh California Islands Symposium* (Ed. by C. C. Damiani & D. K. Garcelon), pp. 293–300. Arcata, California: Institute for Wildlife Studies.

Levey, D. J. & Stiles, F. G. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *American Naturalist*, **140**, 447–476.

MacArthur, R. H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. New York: Harper & Row.

Martin, P. R. & Martin, T. E. 2001. Behavioral interactions between coexisting species: song playback experiments with wood warblers. *Ecology*, **82**, 207–218.

Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. & Fontaine, J. J. 2000. Parental care and clutch sizes in North and South American birds. *Science*, **287**, 1482–1485.

Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright future? *Auk*, **121**, 289–301.

McGregor, P. K. 1992. Quantifying responses to playback: one, many, or composite multivariate measures. In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 79–96. New York: Plenum.

McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, J. B., Fusani, L., Gerhardt, J. C., Gilbert, F., Horn, A. G., Klump, G. H., Kroodsma, D. E., et al. 1992. Design of playback experiments: the Thornbridge Hall NATO ARW consensus. In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 1–9. New York: Plenum.

Mennill, D. J. & Ratcliffe, L. M. 2000. A field test of Syrinx sound analysis software in interactive playback. *Bioacoustics*, **11**, 77–86.

Müller, C. A. & Manser, M. B. 2007. 'Nasty neighbours' rather than 'dear enemies' in a social carnivore. *Proceedings of the Royal Society B*, **274**, 959–965.

Newey, P. S., Robson, S. K. A. & Crozier, R. H. 2008. Weaver ants *Oecophylla smaragdina* encounter nasty neighbors rather than dear enemies. *Ecology*, **91**, 2366–2372.

Porneluzi, P. A. & Faaborg, J. 1999. Season-long fecundity, survival, and viability of ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology*, **13**, 1151–1161.

Pratt, A. E. & McLain, D. K. 2006. How dear is my enemy: intruder–resident and resident–resident encounters in male sand fiddler crabs (*Uca pugilator*). *Behaviour*, **143**, 597–617.

Price, K., Boutin, S. & Ydenberg, R. 1990. Intensity of territorial defense in red squirrels: an experimental test of the asymmetric war of attrition. *Behavioral Ecology and Sociobiology*, **27**, 217–222.

Pyle, P. 1997. *Identification Guide to North American Birds: Part 1*. Bolinas, California: Slate Creek Press.

Ricklefs, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk*, **97**, 38–49.

Ricklefs, R. E. & Wikelski, M. 2002. The physiology/life-history nexus. *Trends in Ecology & Evolution*, **17**, 462–468.

Roff, D. A. 2002. *The Evolution of Life Histories*. New York: Chapman & Hall.

Sillett, T. S. & Holmes, R. T. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, **71**, 296–308.

Sillett, T. S., Rodenhouse, N. L. & Holmes, R. T. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology*, **85**, 2467–2477.

Smith, S. M. 1978. The 'Underworld' in a territorial sparrow: adaptive strategy for floaters. *American Naturalist*, **112**, 571–582.

Sogge, M. K., Gilbert, W. M. & Riper, C. V., III 1994. Orange-crowned warbler (*Vermivora celata*). In: *The Birds of North America. No. 101* (Ed. by A. Poole & F. Gill). Philadelphia: Academy of Natural Sciences, Washington, D. C.: American Ornithologists' Union.

Stamps, J. A. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior*, **23**, 173–232.

Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Temeles, E. J. 1990. Northern harriers on feeding territories respond more aggressively to neighbors than to floaters. *Behavioral Ecology and Sociobiology*, **26**, 57–63.

Temeles, E. J. 1994. The role of neighbours in territorial systems: when are they 'dear enemies'? *Animal Behaviour*, **47**, 339–350.

Trivers, R. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35–57.

Whiting, M. J. 1999. When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. *Behavioral Ecology and Sociobiology*, **46**, 210–214.

Wilson, E. O. 1975. *Sociobiology: the New Synthesis*. Cambridge, Massachusetts: Harvard University Press.

Wingfield, J. C. & Hahn, T. P. 1994. Testosterone and territorial behaviour in sedentary and migratory sparrows. *Animal Behaviour*, **47**, 77–89.

Wingfield, J. C., Hegner, R. E., Jr., Dufty, A. M., Jr. & Ball, G. F. 1990. The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, **136**, 829–846.

Wingfield, J. C., Lynn, S. E. & Soma, K. K. 2001. Avoiding the 'costs' of testosterone: ecological bases of hormone–behavior interactions. *Brain, Behavior, and Evolution*, **57**, 239–251.

Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581–584.

Ydenberg, R. C., Giraldeau, L.-A. & Falls, J. B. 1988. Neighbors, strangers, and the asymmetric war of attrition. *Animal Behaviour*, **36**, 343–347.

Zack, S. & Stutchbury, B. J. 1992. Delayed breeding in avian social-systems: the role of territory quality and floater tactics. *Behaviour*, **123**, 194–219.