Behav Ecol Sociobiol (2009) 63:731–739
DOI 10.1007/s00265-008-0706-1

ORIGINAL PAPER

Love thy neighbour? Social nesting pattern, host mass and nest size affect ectoparasite intensity in Darwin's tree finches

Sonia Kleindorfer · Rachael Y. Dudaniec

Received: 7 December 2008 / Accepted: 15 December 2008 / Published online: 20 January 2009

Abstract Social nesting behaviour is commonly associated with high prevalence and intensity of parasites in intraspecific comparisons. Little is known about the effects of interspecific host breeding density for parasite intensity in generalist host–parasite systems. Darwin's small tree finch (*Camarhynchus parvulus*) on Santa Cruz Island, Galápagos Islands, nests in both heterospecific aggregations and at solitary sites. All Darwin finch species on Santa Cruz Island are infested with larvae of the invasive blood-sucking fly *Philornis downsi*. In this study, we test the prediction that total *P. downsi* intensity (the number of parasites per nest) is higher for nests in heterospecific aggregations than at solitary nests. We also examine variation in *P. downsi* intensity in relation to three predictor variables: (1) nest size, (2) nest bottom thickness and (3) host adult body mass, both within and across finch species. The results show that (1) total *P. downsi* intensity was significantly higher for small tree finch nests with many close neighbours; (2) finches with increased adult body mass built larger nests (inter- and intraspecific comparison); (3) parasite intensity increased significantly with nest size across species and in the small tree finch alone; and (4) nest bottom thickness did not vary with nest size or parasite intensity. These results provide evidence for an interaction between social nesting behaviour, nest characteristics and host mass that influences the distribution and potential impact of mobile ectoparasites in birds.

Keywords Body mass · Darwin's finches · Ectoparasites · Nesting aggregation · Nest size

Communicated by P. Heeb and T. Czeschlik

S. Kleindorfer · R. Y. Dudaniec
Flinders University,
Bedford Park,
Adelaide 5042, Australia

S. Kleindorfer
e-mail: sonia.kleindorfer@flinders.edu.au

R. Y. Dudaniec (✉)
School of Biological Sciences, Flinders University,
Bedford Park,
Adelaide, South Australia 5042, Australia
e-mail: rachael.dudaniec@gmail.com

Introduction

The study of social nesting behaviour has generated many insights into the costs and benefits of aggregations, but less is understood about the mechanisms underlying their formation (Tinbergen 1964; Clotfelter and Yasukawa 1999). Past studies have focused on identifying the costs and benefits of group living, which were used as post hoc evidence for the cause of the aggregation (e.g., Silva et al. 1994). Despite the logical fallacy of such an argument (Williams 1966), understanding current costs and benefits of aggregations will provide information on the strength of natural and/or sexual selection to maintain them (Aviles 1999). Social nesting behaviour may have not only advantages such as reduced nest predation (Hamilton 1971) but also costs such as higher parasite prevalence and intensity (Brown and Brown 1996; Hoi et al. 1998) or sometimes increased predator attraction (Varela et al. 2007). Parasite intensity is influenced by many factors including the mode of parasite transmission, which will vary in efficacy in relation to host density (reviewed in Fenton et al. 2002; Whiteman and Parker 2004). Evidence suggests that parasites limit host group size for specific parasite transmission modes (because of different transmission efficacy in relation to group size and parasite dispersal),

but at present, there is no evidence that parasite avoidance is the cause of particular patterns of group living (Poulin 1999).

Group living in conspecific birds is associated with a higher probability of acquiring and accumulating contact-transmitted ectoparasites (e.g. mites, feather lice) due to increased proximity and physical contact among group members (Poulin 1991; Brown and Brown 1996). Transmission of mobile ectoparasites, such as blood-sucking flies, is predicted to not differ between group-living and solitary individuals because mobile parasites are not dependent on host contact or proximity for transmission (Poulin 1991), though this prediction is not always supported (Duncan and Vigne 1979). Parasite intensity within groups can show high variation, and some individuals typically have very few or a lot of parasites compared to the mean for the group (reviewed in Wilson et al. 2002). The 'encounter-dilution effect' in relation to host density is known across taxa (in feral horses, Duncan and Vigne 1979; wasps, Wieslo 1984; and sticklebacks, Poulin and Fitzgerald 1989) and is analogous to the predicted decrease in predation probability for individuals within larger groups (e.g. the 'selfish herd' model developed by Hamilton 1971). However, mobile parasites may show the opposite pattern when the probability of parasites detecting hosts increases with host group size and when an individual parasite can affect multiple hosts within host aggregations (Mooring and Hart 1992).

In this study, we examine nesting aggregation in Darwin's tree finches in relation to parasitism by the fly *Philornis downsi* (Muscidae). Darwin's small tree finch (*Camarhynchus parvulus*) nests either with zero to one neighbouring nest within 20 m of the focal nest (referred to as solitary nesting) or with two to four heterospecific nests (referred to as mixed species nesting associations; Kleindorfer et al., unpublished data). Mixed species nesting associations are known for birds but have rarely been studied in relation to parasitism (Burger 1981; Mönkkönen and Forsman 2002). Birds in mixed nesting associations often have lower nest predation (Kleindorfer et al., unpublished data), but studies also suggest that such associations (and large groups in general) may be easier to locate for both predators and parasites (Nicolas and Sillans 1989; Danchin and Wagner 1997). Increased propensity for nesting in mixed nesting associations may therefore represent an 'ecological trap' if fitness consequences of introduced parasites or predators are increased in comparison to solitary nesting (reviewed in Robertson and Hutto 2006).

Larvae of the introduced parasitic fly *P. downsi* cause high fitness costs in Galápagos finches (Fessl and Tebbich 2002; Dudaniec et al. 2006; Fessl et al. 2006a). The parasite was first formally identified from Darwin finch nests in 1997, has 100% prevalence for all Darwin finch species on Santa Cruz Island and occurs on all but two of the 13 major islands (Wiedenfeld et al. 2007). The parasite causes low nestling mass, low haemoglobin concentration (Dudaniec et al. 2006; Fessl et al. 2006a), high blood loss (between 18% and 55%) and low fledging success (19–100% brood loss; Fessl and Tebbich 2002; Fessl et al. 2006b). In 2006, *P. downsi* was given the highest risk rating for introduced species to the Galápagos Islands (Causton et al. 2006) and is a major conservation concern for small and endemic bird populations (Dvorak et al. 2004; Wikelski et al. 2004; Grant et al. 2005).

It is not clear why we see high levels of intraspecific variation in *P. downsi* intensity, though finch species with large adult body mass have more *P. downsi* in their nests (Dudaniec et al. 2006, 2007). While parasite fitness may depend on features such as host mass and immune defence, parasite fecundity does not always covary with host characteristics (e.g. parasitic flies of barn owls: Roulin 1999). Host nest size may help to explain intraspecific variation in parasite intensity, especially if the parasite depends on host nest characteristics (e.g. burrowing depth) for survival (in *Protocalliphora* species, Whitworth 1976; Gold and Dahlsten 1989; Remeš and Krist 2005). Nest size may also affect host quality in terms of immunity, both intra- and interspecifically (Soler et al. 2007). *P. downsi* larvae use the bottom layers of finch nests for refuge and as a substrate for pupariation, whereby densely packed puparia are enclosed by tightly woven cocoons in the nesting material. Therefore, the thickness of the nest bottom layer may be a specific spatial limiting factor for parasite intensity in Darwin's finches.

At an intraspecific level, parasite intensity in birds generally increases with the level of sociality (e.g. colonial nesting species; Côté and Poulin 1995). To date, few studies have examined interspecific variation in social nesting behaviour in relation to parasite intensity for generalist avian parasites (Tella 2002). In this study, we examine Darwin's tree finches on Santa Cruz Island, Galápagos archipelago to test the following predictions: (1) Total *P. downsi* intensity (number of parasites per nest, defined by Bush et al. 1997) is higher for nests in mixed species nesting associations than solitary nests; (2) hosts with high adult body mass build larger nests with increased nest bottom thickness; and (3) *P. downsi* total intensity increases with nest size (within and across finch species) and nest bottom thickness (across finch species).

Materials and methods

Location and study species

This study was conducted on Santa Cruz Island in the highland area surrounding Los Gemelos (0°37′ S, 90°21′ W) during the breeding season (January–March) from 2000 to

2004, excluding 2003. Although Darwin's tree finches occur in both the lowlands and highlands of Santa Cruz Island, they attain their highest density in the highland *Scalesia* zone (300–750 m), an area that is dominated by the endemic composite tree *Scalesia pedunculata* (Asteraceae) (Eliasson 1984). We sampled nests from five species of Darwin's finches: small ground finch, *Geospiza fuliginosa*; warbler finch, *Certhidea olivacea*; small tree finch, *C. parvulus*; large tree finch, *Camarhynchus psittacula*; woodpecker finch, *Cactospiza pallida.* The latter three species are members of the 'tree finch' group and occur either exclusively or at higher density in the highlands, while the small ground finch breeds at higher density in the lowlands (0–100 m) but is common in the highlands (Kleindorfer 2007a). The warbler finch nests exclusively in the highlands.

Nest distance of neighbours

We recorded the location (GPS Garmin 12 XC) and the number of active nests within a 20 m radius per focal small tree finch nest but did not include unused display nests in the analysis (see also Kleindorfer 2007a). Twenty metres was selected as a distance because it is the maximum distance at which males of the small tree finch respond to playback of song by other males (Christensen et al., unpublished data; Kleindorfer, unpublished data). Active nests were identified by males singing at nests, incubation or parents feeding nestlings. Recording the distance of all nests surrounding the focal nest within 20 m was aided by placement of two intersecting 10 m ropes below the focal nest. Decimal longitude and latitude coordinates were transformed into Universal Transverse Mercator coordinates in the form of eastings and northings. These values were then used to calculate the distance between all nests from a common zero point. Distances of all nests from focal small tree finch nests were sorted and could be examined for the cutoff value of 20 m. Because the distribution is bimodal, nests with zero or one neighbour within a 20 m radius were termed solitary nests, and nests with two or more neighbours (range was two to four) were termed mixed species nesting associations (defined in more detail in Kleindorfer et al., unpublished data).

Nest monitoring

Darwin's finches are usually socially monogamous (Grant and Grant 2008) and build domed shaped nests. When breeding commences, males build a display nest and sing to attract a mate (Lack 1947; Kleindorfer 2007a). Females then visit the singing male and often enter and inspect the nest. A female either rejects the male and his display nest, accepts the male and builds a new nest together with the male or accepts both the male and the display nest for nesting (Kleindorfer 2007a). During nest building, males primarily build the outer nest, while females primarily collect nesting material to reinforce the inner bottom layers (S. Kleindorfer, personal observation). We monitored active nests from the first stage of nest building by the male until the nesting outcome was known (Kleindorfer 2007a,b). Nesting phase was determined from repeated 20 min observations (every 2 days) of parental activity at each nest as well as by nest inspection. Active nests were classified into three breeding stages: incubation, early feeding (<6 days post-hatching), and mid- to late feeding (6–12 days post-hatching). We monitored a total of 199 small tree finch nests. For this study, we restrict the sample size to 43 nests that met two criteria: (1) nestlings survived until ≥6 days post-hatching (to minimise the effects of nestling age on variation in total parasite intensity; see Fessl and Tebbich 2002), and (2) accurate information was obtained for the number and proximity of active nests within 20 m of the focal nest (see below; Kleindorfer et al., unpublished data; Table 1). The focal nest was always the small tree finch, *C. parvulus*, and for analyses of nesting pattern (mixed species versus solitary nesting) and parasite

Table 1 Total *P. downsi* intensity (number of parasites per nest) across five Darwin finch species in relation to host nest characteristics

	Warbler finch	Small tree finch	Small ground finch	Large tree finch	Woodpecker finch
Sample size	9	17	9	4	4
Adult body mass (g)[a]	9.4	12.2	13.3	16.7	22.0
Parasite intensity	41±6	23±3	33±3	39±9	57±4
Nest height (cm)	11.2±0.3	13±0.3	14.4±0.3	16.4±0.4	16.5±0.4
Nest width (cm)	8.9±0.4	9.8±0.3	10.2±0.3	12.8±0.3	13.3±0.4
Nest entrance (cm)	4.2±0.1	4.6±0.1	5.2±0.3	7.6±0.2	8±0.5
Nest bottom (cm)	3.44±0.2	4.12±0.2	4.22±0.4	4.88±0.3	5.13±0.4
% Vegetation cover	44.2±3.4	53.2±2.9	45.6±3.5	42.5±4.8	41.3±7.5
Nesting height (m)	4.2±0.4	6.2±0.3	4.1±0.4	6.9±0.2	6.5±0.2

We show sample sizes for nests at which nestlings survived to ≥6 days post hatching and for which we have data on the distance of all neighbouring nests and species summaries for nest size variables (shown as means±SE)

[a] Adult body mass (mean) was not calculated from the birds sampled in this study and are taken from Dudaniec et al. (2007)

intensity, only intensity of the focal nest was used. Data on *P. downsi* intensity were also collected from nests of four other finch species in which nestlings survived ≥6 days post-hatching that were also members of mixed associations (Table 1). We do not have data for solitary nests for these species because our comparison of *P. downsi* intensity in mixed nesting associations versus solitary nests is for the small tree finch only.

Nest size and nest site characteristics

After the nesting attempt was completed, we collected each nest and measured the following variables: (1) nest height (cm), (2) nest width (cm), (3) diameter of the entrance (cm) and (4) thickness of the nest bottom (cm) (measured by placing a ruler from the top of the nest to the base of inside of the entrance hole, and subtracting this length from the nest height). We also measured the following nest site characteristics: height of the nest (m) in the nesting tree and percentage of leaf cover above, below and to the sides of the nest, which was visually estimated as a percentage of each nest surface area covered 1 m to each side of the nest. For the analysis, we used the mean percentage nest cover per nest.

Parasite life history and collection

P. downsi is an obligate avian parasite in its three larval stages, whereas adult flies feed on organic matter (Fessl and Tebbich 2002; Dudaniec and Kleindorfer 2006). The fly is oviparous, and larval development is triggered by carbon dioxide (Muth 2007). First instar fly larvae are found in nestling nares after 8–24 h post-hatching (Fessl et al. 2006b). Mature second and third instar larvae attach externally and feed on nestling blood and tissues (Dudaniec and Kleindorfer 2006; Fessl et al. 2006b). The larvae feed for about 4 to 6 days before pupating in tight clusters at the base of the nesting material for approximately two weeks (Dudaniec and Kleindorfer 2006). Most larvae of *P. downsi* reach their third instar phase at the time of host fledging. All nests (100%) with nestlings ≥6 days contained *P. downsi* larvae, puparia or puparia cases. Inactive nests were stored in individual sealed plastic bags and subsequently dismantled to count the number of parasites from the thick nest bottom layers (Fessl and Tebbich 2002). *P. downsi* puparia, puparia cases, second and third instar larvae are easily detected and collected from nests, whereas first instars are rarely found in the nesting material (Wiedenfeld et al. 2007; R. Dudaniec, personal observation).

Statistical analysis

Summary statistics are presented as means±SE. All statistical tests are two-tailed. Data for total *P. downsi* intensity met the underlying assumption for normality and were not transformed. Nest site concealment data were calculated as percentages and were arcsine square root transformed. We used principal components analysis (PCA) with varimax rotation method to reduce the two nest size variables (nest width, nest height) to one derived variable with an eigenvalue of 1.9 that explained 94% of the variance (factor loadings were 0.97 and 0.97 for nest height and width respectively). We examined nest bottom thickness as a separate variable. We used analysis of variance (ANOVA) to examine *P. downsi* intensity across species and in relation to nesting pattern. The residuals of the ANOVA were normally distributed. We used multiple regression analysis to examine the role of the derived nest size variable (PCA1), nest bottom thickness, nest vegetation cover, nesting height and the number of neighbouring nests for *P. downsi* total intensity. Sample size was inadequate to analyse adult size and body mass with nest parasite intensity. All analyses were performed using SPSS 14.0 for Windows.

Results

Heterospecific nesting density

No nests of the focal species (small tree finch, *C. parvulus*) were found within 20 m of another small tree finch nest; therefore, all nearest neighbours within 20 m were heterospecific. The majority of nests at which nestlings survived until ≥6 days post-hatching (65%) were in mixed species nesting associations (28/43), while the rest were classified as solitary nests (15/43; 35%). Using ANOVA, we examined parasite intensity in relation to host species and nesting pattern (mixed versus solitary nests). Intensity of infestation by *P. downsi* differed significantly across host species ($F_{4,\ 42}=5.06$, $P=0.003$) and was highest in woodpecker finch>warbler finch> large tree finch>small tree finch>small ground finch (Table 1). Nesting pattern was significantly related to parasite intensity ($F_{1,\ 42}=7.3$, $P=0.011$) but not the interaction term host species×nesting pattern ($F_{4,\ 42}=0.7$, $P=0.573$). Thus, nests with many neighbours had more parasites per nest than solitary nests (Fig. 1), and host species composition within the nesting aggregations did not covary with parasite intensity.

Nest size, nest bottom thickness and parasite intensity

Nest size differed significantly across species in proportion to adult body mass; that is, small species had small nest size and large species had large nest size (Fig. 2) ($r=0.88$, $t=11.5$, $P<0.001$). Using the derived nest size variable (PCA1), we found a significant correlation between nest size and *P.*

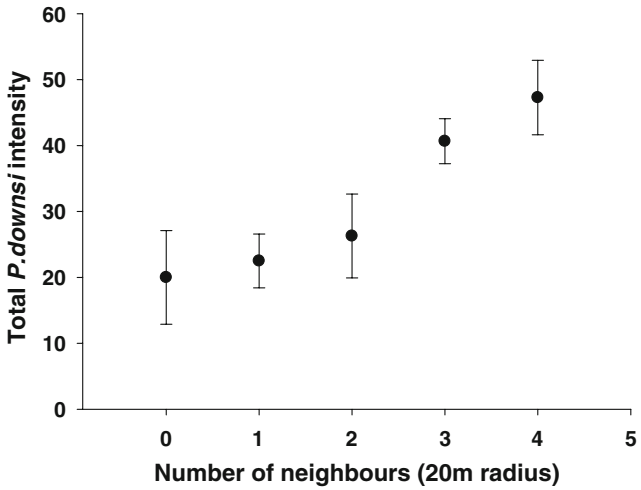

Fig. 1 Total *P. downsi* intensity (mean±SE) of the focal small tree finch nest increases with the number of neighbours within a 20 m radius (n=43 nests)

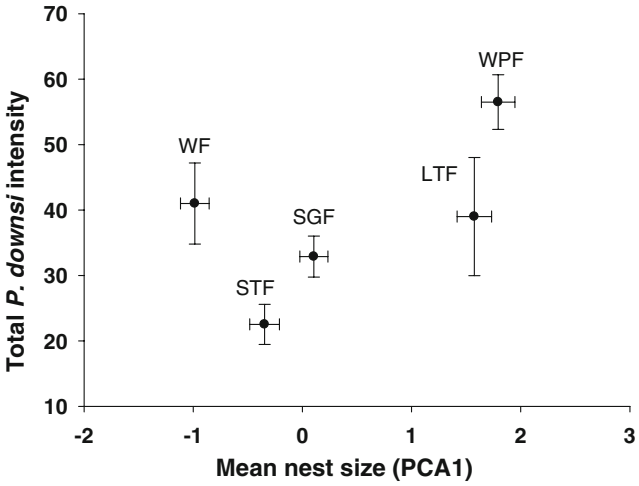

Fig. 3 Total *P. downsi* intensity (mean±SE) increases with nest size (±SE) (derived PCA variable). The species abbreviations are *WF* warbler finch, *SGF* small ground finch, *STF* small tree finch, *LTF* large tree finch and *WPF* woodpecker finch

downsi intensity (b=0.4, $t_{1,\ 41}$=2.9, P=0.006; Fig. 3). Within the small tree finch only, there was a significant positive correlation between nest size and *P. downsi* intensity (b=0.6, $t_{1,\ 15}$=3.0, r=0.6, P=0.009; Fig. 4). However, there was no significant relation between nest bottom thickness and *P. downsi* intensity across species (b=0.1, $t_{1,\ 41}$=0.5, r=0.1, P=0.646) or with nest size (PCA1) within species (linear regression, all species, P=0.397–0.886).

Multivariate approach: nesting density and nest size

Table 2 shows the results of a multiple regression analysis to examine total *P. downsi* intensity in relation to the derived nest size variable (PCA1), percentage vegetation cover at the nest, nesting height and the number of neighbours within a 20 m radius. Both nest size and the number of neighbours were significant predictors of total *P. downsi* intensity.

Discussion

P. downsi intensity was higher for nests in mixed species nesting associations (65% of nests) than solitary nests (35% of nests) and increased with the number of neighbouring nests surrounding the focal small tree finch nest (Fig. 1). This association was unaffected by the species composition of neighbouring nests. Because we only included nests that

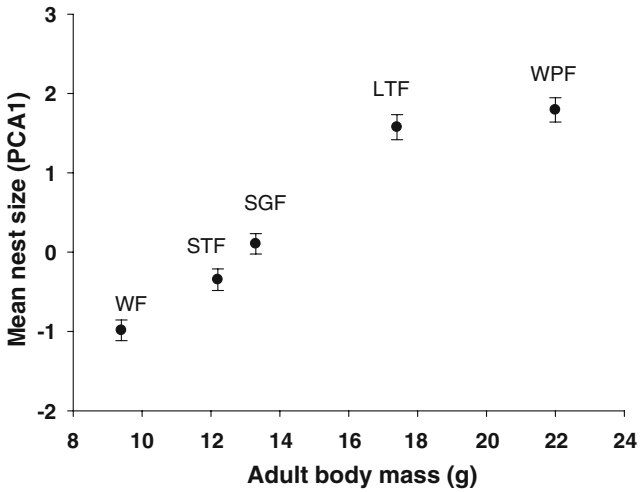

Fig. 2 The positive relation between host adult body mass (g) (mean per species) and mean nest size (±SE) (derived PCA variable). The species abbreviations are *WF* warbler finch, *SGF* small ground finch, *STF* small tree finch, *LTF* large tree finch and *WPF* woodpecker finch

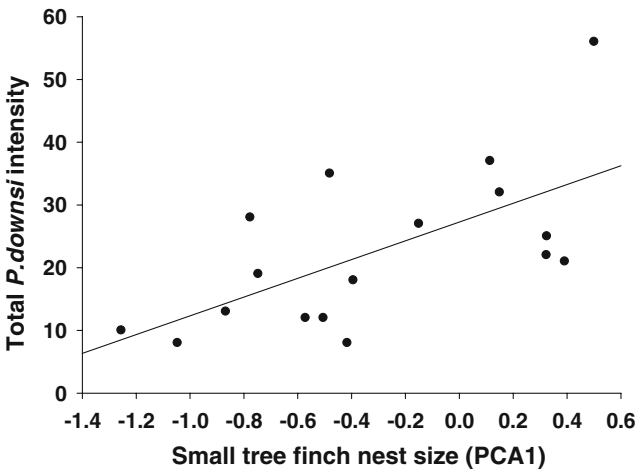

Fig. 4 Data for the small tree finch (*Camarhynchus parvulus*) only: a positive correlation between nest size (derived PCA variable) and total *P. downsi* intensity (number of parasites per nest) (r=0.61, P< 0.02; n=17 nests)

Table 2 Multiple regression results for total *P. downsi* intensity (the number of parasites per nest; dependent variable) against the following independent variables: nest size (derived variable from PCA analysis), nest cover, nesting height and the number of neighbours (within 20 m; n=43)

	B	SE	Beta	*t*	*P* value
Constant	37.97	11.75		3.23	0.003
Nest size (PCA1)	5.64	2.39	0.33	2.36	0.024
Vegetation cover	−0.27	0.18	−0.18	−1.49	0.142
Nesting height	−1.33	1.47	−0.12	−0.90	0.372
Number of neighbours	6.81	1.64	0.50	4.15	0.001

Dependent variable: total *P. downsi* intensity

survived to six days post-hatching for our measure of *P. downsi* intensity and mixed associations had lower nest predation (Kleindorfer et al., unpublished data), we had more nests in mixed associations than solitary ones. However, the percentage of mixed associations and solitary nests was comparable to a previous study (Kleindorfer et al., unpublished data).

Previous experimental and observational studies showed that *P. downsi* causes high nestling mortality (reviewed in Dudaniec and Kleindorfer 2006). Our current finding therefore raises the question: Why do Darwin's tree finches frequently nest in mixed associations given predicted high fitness costs due to parasitism that increase with the size of the nesting aggregation? Our findings may indicate the existence of an ecological trap (Robertson and Hutto 2006), in which the fitness benefits of nesting in aggregations (e.g. increased predator vigilance) have been overcome by increased impacts of a recently introduced parasite. Ecological traps triggered by sudden changes that result in high fitness costs may initiate rapid population decline (Robertson and Hutto 2006).

Mixed nesting associations are composed of between two and four species, and all contain a nest of one large finch species (Kleindorfer et al., unpublished data)—either a large tree finch or woodpecker finch nest. Notably, parasite intensity was highest for large finch species, and host body mass and nest size were both covariates of *P. downsi* intensity (large birds built big nests) (Fig. 2). Within the small tree finch, larger males built larger nests, and larger nests had higher *P. downsi* intensity (Figs. 3 and 4). We could not directly examine small tree finch adult body size and mass with *P. downsi* intensity due to small sample size (only four nests). The interspecific differences in parasite intensity within mixed associations may be indicative of 'apparent competition' (Holt and Kotler 1987), whereby indirect interactions between one host species and another are formed in response to survival costs from a mutual parasite. However, this interaction is largely determined by parasite behaviour and requires further examination (Holt and Kotler 1987).

Nest bottom thickness is an important substrate for the puparia of *P. downsi*. However, nest bottom thickness was not significantly correlated with nest size and did not significantly predict *P. downsi* intensity. Combined, these findings suggest that host body mass and social nesting pattern are important causal agents in *P. downsi* intensity but not nest size or bottom thickness.

Host nesting behaviour and parasitism

Social nesting aggregations not only have many benefits (e.g. increased predator vigilance, opportunity for extra-pair copulations) but are also frequently associated with increased resource competition, increased conspicuousness to predators and a higher risk of disease transmission (Danchin and Wagner 1997; Wagner 1997; Richardson and Bolen 1999). Nesting aggregations in territorial species can reflect local variation in resource densities. For example, the presence of established males or of dominant conspecifics in an area may act as an indicator of habitat quality for individuals acquiring their first territory (Stamps 1988; Robertson and Hutto 2006). In Darwin's tree finches, nest site vegetation characteristics were not predictably associated with nesting pattern (mixed species versus solitary nesting), while tree finch nests in mixed associations had a higher nest defence response and reduced predation compared with solitary nests (Robertson et al., unpublished data).

Previous research has focused on the mechanisms for how parasites may disrupt or modify host social systems to favour the expression of social or anti-social behaviour (Mooring and Hart 1992; O'Donnell 1997; Sorci et al. 1997). Larger colony size and high ectoparasite intensity were associated with increased levels of corticosterone in cliff swallows (Raouf et al. 2006), which can impair reproductive or cognitive function. The cost of ectoparasitism for host reproductive success increased with colony size in the family Hirundinidae; yet, this was countered by a greater investment in immune function among highly colonial species, particularly in nestlings (Møller et al. 2001). Selective pressures on host social behaviour may be exacerbated, or altered by

parasitism, but they are likely to vary considerably with the hosts' parasite defence mechanisms, parasite life history and the influence of other ecological pressures (e.g. resource availability and predation).

Parasite transmission and host grouping behaviour

Because *P. downsi* is not a contact-transmitted parasite, theory predicts that the risk of transmission in mixed nesting associations is not likely to exceed the risk to the population as a whole. Therefore, neither solitary nor grouping behaviour should be disfavoured (O'Donnell 1997). In support of this, an inter-specific comparison of 45 passerines by Poulin (1991) showed that group-living species had a greater prevalence of contact-transmitted mites than solitary species, but the abundance of mobile parasitic flies (Hippoboscidae) did not differ with social behaviour. However, mobile parasites may have a higher impact within larger host groups when the probability of a parasite detecting its host increases with host group size and where an individual parasite can use multiple hosts (Mooring and Hart 1992). This latter argument seems to apply to *Philornis* parasites, which are transmitted via mobile adult flies that have the capacity to parasitise multiple nests (Dudaniec et al., unpublished data).

Parasitic flies may be attracted to a group of hosts via visual or olfactory cues (Gibson and Torr 1999) and/or carbon dioxide emissions (Nicolas and Sillans 1989), which are more concentrated in larger host aggregations. From the parasites' perspective, an encounter with a high density group of hosts represents an efficient opportunity to deposit a maximal number of offspring within a short time period (Mooring and Hart 1992). Though smaller inter-nest distances among colonially nesting birds have been associated with higher intensity of contact-transmitted chewing lice (*Meropoecus* and *Brueelia* spp.; Hoi et al. 1998), analogous investigations involving mobile parasites are lacking, particularly in the absence of knowledge regarding parasite dispersal behaviour.

The spatial distribution of hosts is an important factor for the evolution of dispersal behaviour and host specialisation of parasites (Hoi et al. 1998; Tripet et al. 2002). Our data suggest that *P. downsi* females disperse short distances between nests and deposit larvae in multiple nests within close proximity, which may possibly act as a safeguard against stochastic effects between nests that may jeopardise parasite survival (e.g. nest predation). Alternatively, female flies may invest more offspring within individual nests that occur in areas of high host density to maximise offspring reproductive success upon dispersal. Such parasite dispersal behaviour may partly explain the increased total *P. downsi* intensity for finch nests within mixed species associations. Current investigation into the genetic relatedness between and among *P. downsi* offspring in nests may reveal patterns of fly oviposition behaviour and dispersal (Dudaniec et al., unpublished data; Dudaniec et al. 2008a,b).

Nest characteristics, host mass and parasite intensity

Host adult body mass varied with host nest size across species (Fig. 2), and larger nests had increased parasite intensity. Is host body mass or nest size a stronger predictor for *P. downsi* intensity? Higher parasite intensity with increasing nest size in the small tree finch (Fig. 4) suggests that nest size may limit the number of parasites that can be sustained and may influence the successful growth and survival of *P. downsi* through within-host, density-dependent competition (Hughes et al. 2004). However, nest bottom thickness did not covary with *P. downsi* intensity. Host adult mass is a better predictor of ectoparasite intensity than nest size characteristics, possibly because larger finch species have larger nestlings that provide more resources for parasites (Poulin 1991; Poulin and George-Nascimento 2007).

The relationship between nest size, host mass and parasite intensity is likely to be multi-faceted, as suggested by the high intensity found in nests of the light-bodied, small-nested warbler finch (Fig. 3). The warbler finch had the second highest *P. downsi* intensity across six finch species studied on Santa Cruz Island, despite the observation that large finch species generally had more parasites (Dudaniec et al. 2007). This could reflect interspecific variation in nest-site characteristics and host behaviour that influence parasite susceptibility (Gold and Dahlsten 1989). The nesting biology of warbler finches is largely unstudied. Warbler finch nests occurred within all mixed nesting associations (Kleindorfer et al., unpublished data), which was a significant predictor of increased *P. downsi* intensity. Anecdotal reports indicate that warbler finches may take over newly built nests of heterospecific finches (Lack 1947; S. Kleindorfer, personal observation), thus increasing the variance. A focal nesting study of the warbler finch and fly egg laying behaviour is required to further examine the mechanisms driving the contrary patterns found within this species.

Conclusion

The findings of this study do not support the prediction that mobile, non-contact-transmitted ectoparasite intensity is comparable between group living or solitary hosts (Poulin 1991; Mooring and Hart 1992). We found higher *P. downsi* intensity in aggregated nests and in nests of large hosts. Based on the known benefits of mixed species associations in reducing nest predation, the increased costs of nesting in aggregations as a result of *Philornis* parasitism may balance the costs of solitary versus aggregated nesting (Kleindorfer

et al., unpublished data; Dudaniec et al. 2006). However, if the added costs of mixed species nesting, owing to increased mortality from *P. downsi*, prove to be greater than the benefits from reduced nest predation, then mixed species nesting would constitute an ecological trap (Robertson and Hutto 2006). It is possible that such costs of parasitism will be substantially greater in smaller bodied finches, as these smaller finches have smaller nestlings, which generally exhibit a greater number of parasites per gram of tissue (Dudaniec et al. 2007). Relative to body mass, the warbler finch appears to be particularly vulnerable to *P. downsi*, exhibiting significantly higher levels of parasitism in this study compared with the small tree finch, which is 27% heavier (Table 1). Notably, the warbler finch has been pushed to the brink of extinction on one Galápagos Island, owing at least partially to parasitism by *P. downsi* (Grant et al. 2005). Thus, an informed response to the question of whether mixed species nesting associations present an ecological trap may have to be answered separately for each species of Darwin's finches. Moreover, even small differences in opposing mortality trends may have major ecological and evolutionary consequences, as the cumulative effects of natural selection will tend to magnify the consequences of such differences over multiple generations. Further research on Darwin's finches will be needed to provide a more precise answer to the question of whether mixed species nesting associations constitute an ecological trap—one that, if its existence is confirmed, would represent a serious challenge to the continued survival of this iconic group of birds.

Acknowledgements We thank the Galápagos National Park Service and the Charles Darwin Research Station for the opportunity to work on the Galápagos archipelago. This study was generously funded by the Max Planck Institute for Ornithology and the Austrian Academy of Sciences between 2000 and 2002, with awards to S. Kleindorfer, in 2004 by Flinders University through a Research Establishment Grant, Conservation International and the American Bird Conservancy. TAME airlines provided reduced airfare to the Galápagos. All procedures followed the Guidelines for the Use of Animals in Research (Flinders University, Charles Darwin Research Station, and Galápagos National Parks), the legal requirements of Ecuador, and were approved by the Animal Welfare Committee of Flinders University (permit E189). We thank: Carlos Vinueza, Santiago Torres, Gustavo Jiménez, Rebekah Christensen, and Jeremy Robertson for their dedicated field assistance, Hernan Vargas and David Wiedenfeld for logistical support and Frank J. Sulloway for helpful comments on the manuscript.

References

Aviles L (1999) Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. Evol Ecol Res 1:459–477

Brown CR, Brown MB (1996) Coloniality in the cliff swallow: the effect of group size on social behaviour. University of Chicago Press, London

Burger J (1981) A model for the evolution of mixed-species colonies of Ciconiiformes. Quart Rev Biol 56:143–167

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583

Causton CE, Peck SB, Sinclair BJ, Roque-Albelo L, Hodgson CJ, Landry B (2006) Alien insects: threats and implications for conservation of Galápagos Islands. Ann Entomol Soc Am 99:121–143

Clotfelter ED, Yasukawa K (1999) The effect of aggregated nesting on red-winged blackbird nest success and brood parasitism by brown-headed cowbirds. Condor 101:729–736

Côté IM, Poulin R (1995) Parasitism and group size in social animals: a meta-analysis. Behav Ecol 6:159–165

Danchin E, Wagner RE (1997) The evolution of coloniality: the emergence of new perspectives. Trends Ecol Evol 12:343–347

Dudaniec RY, Kleindorfer S (2006) The effects of the parasitic flies *Philornis* (Diptera: Muscidae) on birds. Emu 106:13–20

Dudaniec RY, Kleindorfer S, Fessl B (2006) Effects of the introduced ectoparasite *Philornis downsi* on haemoglobin level and nestling survival in Darwin's small ground finch (*Geospiza fuliginosa*). Austral Ecol 31:88–94

Dudaniec RY, Fessl B, Kleindorfer S (2007) Interannual and interspecific variation in intensity of the parasitic fly, *Philornis downsi*, in Darwin's finches. Biol Conservat 139:325–332

Dudaniec RY, Gardner MG, Kleindorfer S (2008a) Isolation, characterization and multiplex polymerase chain reaction of novel mircrosatellite loci for the avian parasite *Philornis downsi* (Diptera: Muscidae). Mol Ecol Resources 8:142–144

Dudaniec RY, Gardner MG, Donnellan S, Kleindofer S (2008b) Genetic variation in the invasive avian parasite, *Philornis downsi* (Diptera, Muscidae), on the Galápagos Archipelago. BMC Ecol 8:13–25

Duncan P, Vigne N (1979) The effect of group size in horses on the rate of attacks by blood-sucking flies. Anim Behav 27:623–625

Dvorak M, Vargas H, Fessl B, Tebbich S (2004) On the verge of extinction: a survey of the mangrove finch *Camarhynchus heliobates* and its habitat on the Galápagos Islands. Oryx 38:171–179

Eliasson U (1984) Native climax forests. In: Perry R (ed) Key environments, Galápagos. Pergamon, Oxford, pp 101–114

Fenton A, Fairbairn JP, Norman R, Hudson PJ (2002) Parasite transmission: reconciling theory and reality. J Anim Ecol 71:893–905

Fessl B, Tebbich S (2002) *Philornis downsi*—a recently discovered parasite on the Galápagos archipelago: a threat for Darwin's finches? Ibis 144:445–451

Fessl B, Kleindorfer S, Tebbich S (2006a) An experimental study on the effects of an introduced parasite in Darwin's finches. Biol Conservat 127:55–61

Fessl B, Sinclair BJ, Kleindorfer S (2006b) The life cycle of *Philornis downsi* (Diptera: Muscidae) parasitizing Darwin's finches and its impacts on nestling survival. Parasitology 133:739–747

Gibson G, Torr SJ (1999) Visual and olfactory responses of haematophagous Diptera to host stimuli. Med Vet Entomol 13:2–23

Gold CS, Dahlsten DL (1989) Prevalence, habitat selection, and biology of *Protocalliphora* (Diptera, Calliphoridae) found in nests of mountain and chestnut-backed chickadees in California. Hilgardia 57:1–19

Grant PR, Grant BR (2008) How and why species multiply: The radiation of Darwin's finches. Princeton University Press, Princeton

Grant PR, Grant BR, Petren K, Keller LF (2005) Extinction behind our backs: the possible fate of one of the Darwin's finch species on Isla Floreana, Galápagos. Biol Conservat 122:499–503

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311
Hoi H, Darlova A, König C, Kistofik J (1998) The relations between colony size, breeding density and ectoparasite loads of adult European bee-eaters (*Merops apiaster*). Ecoscience 5:156–163
Holt D, Kotler B (1987) Short-term apparent competition. Am Nat 130:412–430
Hughes WOH, Petersen KS, Ugelvig LV, Pedersen D, Thomsen L, Poulsen M, Boomsma JJ (2004) Density-dependence and within-host competition in a semelparous parasite of leaf-cutting ants. BMC Evol Biol 4:45–56
Kleindorfer S (2007a) Nesting success in Darwin's small tree finch (*Camarhynchus parvulus*): evidence of female preference for older males and more concealed nests. Anim Behav 74:795–804
Kleindorfer S (2007b) The ecology of clutch size variation in Darwin's small ground finch, *Geospiza fuliginosa*: comparison between low and highland habitats. Ibis 149:730–741
Lack D (1947) Darwin's Finches. Cambridge University Press, Cambridge
Møller AP, Merino S, Brown CR, Robertson RJ (2001) Immune defence and host sociality: a comparative study of swallows and martins. Am Nat 158:136–145
Mönkkönen M, Forsman JT (2002) Heterospecific attraction among forest birds: a review. Ornithol Sci 1:41–51
Mooring MS, Hart BL (1992) Animal grouping for protection from parasites: Selfish herd and encounter-dilution effects. Behaviour 123:173–193
Muth A (2007) Control of *Philornis downsi*, bird parasite. Report for Department of Terrestrial Invertebrates, Charles Darwin Research Station
Nicolas G, Sillans D (1989) Immediate and latent effects of carbon dioxide on insects. Ann Rev Entomol 34:97–116
O'Donnell S (1997) How parasites can promote the expression of social behaviour in their hosts. Proc R Soc Lond B 264:689–694
Poulin R (1991) Group-living and infestation by ectoparasites in passerines. Condor 93:418–423
Poulin R (1999) Parasitism and shoal size in juvenile sticklebacks: Conflicting selection pressures from different ectoparasites? Ethology 105:959–968
Poulin R, Fitzgerald GJ (1989) Shoaling as an anti-ectoparasite mechanism in juvenile sticklebacks (*Gasterosteus* spp.). Behav Ecol Sociobiol 24:251–255
Poulin R, George-Nascimento M (2007) The scaling of total parasite biomass with host body mass. Int J Parasitol 37:359–364
Raouf SA, Smith LC, Brown MB, Wingfield JC, Brown CR (2006) Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows. Anim Behav 71:39–48
Remeš V, Krist M (2005) Nest design and the abundance of parasitic *Protocalliphora* blow flies in two hole-nesting passerines. Écoscience 12:549–553
Richardson DS, Bolen GM (1999) A nesting association between semi-colonial Bullock's orioles and yellow-billed magpies: evidence for the predator protection hypothesis. Behav Ecol Sociobiol 46:373–380
Robertson BA, Hutto RL (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085
Roulin A (1999) Fecundity of *Carnus hemapterus* (Diptera), an ectoparasite of juvenile barn owls *Tyto alba*. Alauda 67:205–212
Silva JD, MacDonald DW, Evans PGH (1994) Net costs of group living in a solitary forager, the Eurasian badger (*Meles meles*). Behav Ecol 5:151–158
Soler JJ, Martin-Vivaldi M, Haussy C, Møller AP (2007) Intra- and interspecific relationships between nest size and immunity. Behav Ecol 18:781–791
Sorci G, de Fraipont M, Clobert J (1997) Host density and ectoparasite avoidance in the common lizard (*Lacerta vivipara*). Oecologia 111:183–188
Stamps JA (1988) Conspecific attraction and aggregation in territorial species. Am Nat 131:329–347
Tella JL (2002) The evolutionary transition to coloniality promotes higher blood parasitism in birds. J Evol Biol 15:32–41
Tinbergen N (1964) On aims and methods of ethology. Zeitschrift für Tierpsycholie 20:410–433
Tripet F, Christe P, Møller AP (2002) The importance of host spatial distribution for parasite specialization and speciation: a comparative study of bird fleas (Siphonaptera: Ceratophyllidae). J Anim Ecol 71:735–748
Varela SAM, Danchin E, Wagner RH (2007) Does predation select for or against avian coloniality? A comparative analysis. J Evol Biol 20:1490–1503
Wagner RH (1997) Hidden leks: sexual selection and the clustering of avian territories. In: Parker PG, Burley N (eds) Avian reproductive tactics: female and male perspectives. Ornithol Monog 49:123–145
Whiteman NK, Parker PG (2004) Effects of host sociality on ectoparasite population biology. J Parasitol 90:939–947
Whitworth TL (1976) Host and habitat preferences, life history, pathogenicity and population regulation in species of *Protocalliphora* Hough (Diptera: Calliphoridae). PhD dissertation, Utah State University, Logan, UT
Wiedenfeld DA, Jiménez UGA, Fessl B, Kleindorfer S, Valarezo JC (2007) Distribution of the introduced parasitic fly *Philornis downsi* (Diptera, Muscidae) in the Galápagos Islands. Pac Conservat Biol 13:14–19
Wieslo WT (1984) Gregarious nesting of a digger wasp as a "selfish herd" response to a parasitic fly (Hymenoptera: Sphecidae; Diptera: Sacrophagidae). Behav Ecol Sociobiol 14:157–160
Wikelski M, Foufopoulos J, Vargas H, Snell H (2004) Galápagos birds and diseases: invasive pathogens as threats for island species. Ecol Soc 9 (1), article 5. http://www.ecologyandsociety.org/vol9/iss1/art5
Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton
Wilson K, Bjørnstad ON, Dobson AP, Merler G, Poglayen G, Randolph SE, Read AF, Skorping A (2002) Heterogeneities in macroparasite infections: patterns and processes. In: Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (eds) The ecology of wildlife diseases. Oxford University Press, Oxford, pp 1–48