Interspecific variation in avian blood parasites and haematology associated with urbanization in a desert habitat

H. Bobby Fokidis, Ellis C. Greiner and Pierre Deviche

H. B. Fokidis (correspondence) and P. Deviche, School of Life Sciences, Arizona State University, Tempe, Arizona, 85287, USA. Email: bfokidis@asu.edu. – E. C. Greiner, Department of Infectious Diseases and Pathology, College of Veterinary Medicine, University of Florida, Gainesville, Florida, 32611, USA.

Many avian species are negatively impacted by urbanization, but other species survive and prosper in urbanized areas. One factor potentially contributing to the success of some species in urban areas is the reduced presence of predators or parasite vectors in urban compared to rural areas. In addition, urban areas may provide increased food and water resources, which can enhance immune capacity to resist infection and the ability to eliminate parasites. We determined patterns of blood parasitism, body condition, and immune cell profiles in urban and rural populations of five adult male songbird species that vary in their relative abundance within urban areas. Urban birds generally exhibited less blood parasitism than rural birds. This difference was particularly evident for the urban-adaptable Abert's towhee *Pipilo aberti*. In contrast, no difference in haemoparasitism was seen between urban and rural populations of the curve-billed thrasher *Toxostoma curvirostre*, a less-urban adaptable species. In two closely related species, the curve-billed thrasher and the northern mockingbird *Mimus polyglottos*, urban birds had a higher leukocyte count and a higher heterophil to lymphocyte ratio, which is often associated with chronic stress or current infection, than rural birds. Urban northern mockingbirds were in better condition than rural counterparts, but no habitat-related differences in condition were detected for other species. Parasitic infection was correlated with body condition in only one species, the canyon towhee *Pipilo fuscus*. Parasitic infection in most species was correlated with changes in leukocyte abundance and profile. The findings suggest that interspecific differences in parasitic infection cannot be attributed entirely to differences in vector abundance or body condition. Interactions between immune function, parasite infection risk, and resource availability may contribute to determining the relative ability of certain species to adapt to cities.

For many species, the ability to respond to anthropogenic disturbance, such as urban development, is likely to be an important factor governing their long-term survival. Recently, biologists have become increasingly attracted to urban areas as "natural experiments" where drastic environmental changes alter the native community structure (Emlen 1974, Clergeau et al. 1998, Green and Baker 2003). These changes in community structure are based on species-specific responses to the novel or fractured habitats created by urbanization and likely represent the sum of ecological factors and underlying differences in the biology of these species.

Factors influencing population changes have received considerable attention, particularly in birds. Compared to individuals in native (rural) environments, urban birds are exposed to many potentially detrimental factors including increased brood parasitism (Chace et al. 2003, Burhans and Thompson 2006), human disturbance (Fernandez-Juricic et al. 2001), noise (Slabbekoorn and Peet 2003), feral predation (Woods et al. 2003, Baker et al. 2005), introduced competitors (White et al. 2005), exposure to toxins (Eens et al. 1999), artificial lighting (Longcore and

Rich 2004), and warmer temperatures (Luniak et al. 1990). These factors may influence the health of urban bird populations and, in turn, their relative success at colonizing urban habitats. However, avian species that persist in cities often are exposed to lower predation risk (Gering and Blair 1999), and have access to more food and water resources than species in natural habitats (Shochat et al. 2004). Decreased parasitism may also influence the success of certain avian species in urban areas (Drake 2003, Liu and Stiling 2006). Avian blood parasites may play important roles in sexual selection (Hamilton and Zuk 1982, Cox 1989) and reproductive success (Bonier et al. 2007), but how they affect host fitness remains debated (Cox 1989, Weatherhead and Bennett 1991, Norris and Evans 2000).

The Sonoran Desert of the southwest United States has become a model ecosystem for studying the impacts of urbanization on flora and fauna, largely due to the rapid rates of suburban housing development. The Sonoran Desert is temporally variable with respect to resource availability and this is largely dependent on the annual bimodal pattern of rainfall (Webb et al. 1978, Lauenroth and Sala 1992, Vleck 1993). In contrast, urban areas in this

region have year-round water (such as artificial ponds and canals, swimming pools, sprinkler outflow, and wildlife feeders) and more predictable food resources (such as birdseeds, nectar from exotic vegetation, garbage, and pet food) that may buffer seasonal components of the native habitat. This increased predictability has attracted some native desert bird species to exploit city resources (Green and Baker 2003), although for some species resources may be decreased (Schoech and Bowman 2001). Increased access to nutritional resources may influence the ability to combat parasitic infection because maintenance of immune function is considered energetically and nutritionally costly (Demas et al. 1997, Lochmiller and Deerenberg 2000, but see Klasing and Leshchinsky 1999). This can act to increase the ability of city birds to combat infection.

In addition, exposure to city-associated challenges may negatively impact immune function, perhaps through an increase in circulating glucocorticoids that are released in response to stress (Partecke et al. 2006, Bonier et al. 2007) or through exposure to environmental toxins (Eeva et al. 2005). Furthermore, the presence of water in urban areas may increase the abundance of parasite-transmitting dipteran vectors with aquatic larvae (Marquardt et al. 2000). The dependence of these vectors on water suggests that birds in arid ecosystems typically have low blood parasite prevalence, but recent work refutes this idea (Deviche et al. 2005). The presence of standing water in cities may increase the risk of parasitic infection for urban birds and thus necessitates increased energy allocation to immune maintenance.

We investigated blood parasite infection, body condition (stored energy reserves), and hematology in four native and one introduced species of passerine birds that vary in their occurrence in metropolitan Phoenix, Arizona (Green and Baker 2003), by comparing rural and urban populations. We predicted that urban-adaptable birds have fewer parasite infections than rural birds due to decreased abundance of species-specific vectors in urban areas. We also predicted that urban-adaptable species are more adept at exploiting resources within the city, resulting in better body condition and a greater capacity to fight infection than less adaptable species. However, cities can also serve as ''sink habitats'' for poor-quality birds which utilize marginal urban habitat,

often resulting in higher population densities than in higher-quality habitats (Pulliam 1988). ''Sink'' or ''floater'' populations are often characterized by birds exhibiting decreased reproductive success (Pulliam 1988, Heltzel and Earnst 2006) and lowered body condition (Pulliam 1988, Lambrechts et al. 2004). Our study of body condition may offer some insight into potential source-sink dynamics in this arid region city ecosystem.

Haematological parameters, traditionally used as health indicators for domestic animals, provide useful information for assessing the relative health of wild animal populations (Latimer and Bienzle 2000). The distribution and relative abundance of leucocytes also provides an easy, inexpensive measure of integrated immune function (Salvante 2006). The ability to maintain high numbers of leucocytes prepares an individual for fighting infection, but the production of these cells can also increase in response to current infection (Salvante 2006). To distinguish between these two alternatives we compared the leucocyte profiles and body condition of parasite-infected individuals with those that did not have detectable parasites in both urban and rural habitats. We predicted that: (1) urban-adapted species will have lower prevalence of blood parasites than rural birds, (2) non-parasitized urban individuals will be in better body condition than rural individuals, and (3) parasitized urban individuals will have higher blood leucocyte concentrations than rural birds. Previous studies demonstrated differences in hematological parameters in birds across an urban-rural gradient (Gavett and Wakeley 1986, Ruiz et al. 2002, Bonier et al. 2007), but this study is the first to examine how blood parasitism, body condition, and immunity covary across species in an urban versus rural setting.

Methods

Defining adaptability, bird sampling, and sample preparation

We measured blood parasite infections and hematological parameters in five adult male songbird species (Table 1). An introduced ''urban-exploiter'' (Blair 1996, McKinney 2002), the house sparrow (HOSP; *Passer domesticus*), two pairs of closely related native species from the family

Table 1. Classifications of five Sonoran Desert bird species with respect to their tolerance to urbanization in Phoenix (based on Green and Baker 2003), and sampling effort per life-history stage and locality (sample sizes in parentheses).

Species	Classification		Pre-breeding (n)	Breeding (n)	Post-breeding (n)	Locality (n)
Abert's towhee (ABTO)	Urban-adaptable	Rural	10	18	4	A (27), B (5)
Pipilio aberti		Urban	6	13	5	C (4), D (13), E (7)
Canyon towhee (CANT)	Urban-avoider	Rural	3	9	3	F (13), G (2)
Pipilio fuscus						
Northern mockingbird (NOMO)	Urban-adaptable	Rural	4	4	2	F (4), G (6)
Mimus polyglottos		Urban	5	11	7	C (5), D (11), E (7)
Curve-billed thrasher (CBTH)	Urban-avoider	Rural	5	14	4	A (6), F (3), G (14)
Toxostoma curvirostre		Urban	5	12	5	C (2), D (12), E (8)
House sparrow (HOSP)	Urban-exploiter	Rural	4	8	5	B (17)
Passer domesticus		Urban	7	14	8	C (5), D (9), E (15)

A = Robbin's Butte WMA, B = Red Cone Ranch, C = West Phoenix, D = Central Phoenix, E = East Phoenix, F = Hell's Canyon WA, G = Sierra Estrella WA.

Mimidae: northern mockingbird (NOMO; *Mimus polyglottos*) and curve-billed thrasher (CBTH; *Toxostoma curvirostre*), and two towhee species: Abert's towhee (ABTO; *Pipilo aberti*), and canyon towhee (CANT; *Pipilo fuscus*). The latter four species in central Arizona are common, sedentary, and territorial year-round (Derrickson and Breitwisch 1992, Tweit and Finch 1994, Johnson and Haight 1996, Tweit 1996). In contrast, the HOSP is a sedentary, gregarious species which is closely associated with human activities and, indeed, its distribution in Arizona is entirely restricted to human-populated areas (Lowther and Cink 1992).

Using published data on mean bird density (birds/km^2) in Phoenix, Arizona and outlying desert areas (Green and Baker 2003), native species that were present at significantly higher densities in cities than in native habitats were defined as "urban-adaptable", whereas species present at lower densities in cities than in the native desert were defined as "urban-avoiders" (Table 1; Blair 1996, McKinney 2002). It should be noted that CBTH are commonly found within Phoenix, but their distribution is largely limited to the city's periphery (HBF pers. obs.). This suggests that their presence in the city results from these birds being pushed further from the ancestral city center as human inhabitation expanded, and thus there may be only limited breeding within the city. However, this hypothesis has not been investigated.

We sampled birds from various localities within metropolitan Phoenix (Table 1). These localities included a random sample of high- and low-income residential housing tracts, as well as commercial areas, business districts, and city parks of varying sizes (urban sites). We also sampled three sparsely populated Sonoran desert localities to the southwest of Phoenix and these constituted our rural sites (Table 1). All localities are no more than 25 km apart and were between 33°18′N and 33°57′N, and 111°59′W and 112°41′W. We sampled HOSP within the metropolitan Phoenix area and a rural dairy ranch. Both localities are associated with human habitation and the presence of standing water, however the rural ranch locality is characterized by a lower presence of people and associated activities than within the city. Thus, we included HOSP from both urban and rural sites to offer some insight into how factors besides human-habitation can influence bird physiology.

Birds were caught into mist-nets passively (HOSP) or using conspecific song playback recordings (other species). Sampling was carried out from Jan. to Oct. 2006 and each locality was sampled on a weekly basis. All captures took place between 05.00 and 11.30 h and no diel effects were observed for any variable examined (data not shown). Birds were removed from the net within 3 min of capture and no more than 500 µl of blood was collected from the right jugular vein using a heparinized 0.3 cc syringe with a 29.5 gauge needle. Blood was collected as part of another study examining hormone levels and the actual volume of blood drawn varied among species. Approximately 5 µl of blood was used to prepare thin blood smears on glass microscope slides (Bennett 1970, Deviche et al. 2001, Walberg 2001). Smears were air-dried at ambient temperature and stored until fixation. Males were identified by plumage in the case of HOSP and either by the presence of a developed cloacal protuberance in males during the breeding season or by unilateral laparotomy during the non-breeding season, for the other four species. Laparotomies were done under local lidocaine-induced topical anesthesia following guidelines approved by the Arizona State University Institutional Animal Care and Use Committee. During laparotomies we measured testis length to the nearest 1 mm. Age (hatch-year, HY; after-hatch year, AHY) was determined using flight feather and rectrix characteristics and the degree of skull pneumatization (Pyle 1997). We also recorded whether birds were molting. These measures enabled us to classify sampled birds as being in pre-breeding condition, breeding condition, or post-breeding condition (i.e., molting). Male birds were considered in breeding condition if their testis length exceeded half the maximum average length observed for each species during the breeding season. This threshold value was based on the conservative assumption that testes can produce sperm when at half-maximal volume (Partecke et al. 2004). To assess body condition, body mass (± 0.1 g) and tarsus length (± 1 mm) were measured. Birds were fitted with a uniquely numbered aluminum US Geological Survey leg band and were released at the capture site.

Blood parasites and leucocyte profiles

Blood smears were fixed for 10 min in absolute methanol within 5 days of collection and stained using the Giemsa method (Bennett 1970). Stained smears were dehydrated for one week under partial vacuum and then cleared using xylene. Slides were coverslipped and sealed using Cytoseal 60 (VWR, San Francisco, California) for long-term storage.

Parasite prevalence, defined as the percentage of infected individuals in a sample (Bush et al. 1997), was determined by surveying blood smears at $250 \times$ magnification for 10 min and then at $400 \times$ magnification for 5 min using an Olympus BX60 light microscope (Olympus Optical Co., Tokyo). Slides were examined by a single observer (HBF) without knowledge of locality, species, or time of year that samples were collected. The density of infection with microfilariae and *Trypanosoma* was calculated as the number of parasites seen per unit of area (Bush et al. 1997). For this, we located large areas of the slide that had a relatively homogenous cell density and were about one cell layer thick. Then 200 randomly chosen microscope fields within this area were examined at $400 \times$ magnification and the number of each parasite type encountered was counted. To determine observer repeatability 12 randomly chosen slides from multiple species were each analyzed three times and parasite numbers were compared using Kendall's coefficient of concordance (Siegel 1956). Only the number of microfilariae could be statistically tested and this was highly consistent (W $= 0.992$, P < 0.001). The number of parasite types detected on each smear was identical between observations.

To quantify the density of *Haemoproteus* infection, 25 non-overlapping microscope fields that contained non-overlapping single cell layers were digitized at $400 \times$ magnification. Image-Pro version 4.1 software (Media Cybernetics, Silver Springs, Maryland) was used to identify 10,000 erythrocytes per sample (Godfrey et al. 1987,

Gering and Atkinson 2004). Erythrocytes were identified based on morphological characteristics of their nucleus (aspect ratio, length, width, perimeter, roundness, relative brightness, and color) and were included in the counts if their entire nucleus was visible on the digitized image. *Haemoproteus*-infected erythrocytes seen on digitized images were manually counted and parasite densities were expressed as the number of *Haemoproteus* per 10,000 erythrocytes. The study of blood smears using light microscopy to detect blood parasites is not sensitive enough to conclude that individuals without visual evidence of parasites are parasite-free (Fallon et al. 2003) because subpatent infections may escape detection (Jarvi et al. 2001). Recently, Bentz et al. (2006) reported that blood smears may only detect relatively high parasitemia, suggestive of intense infection. Although this is an important concern, the above method does provides a relative measure of the degree of infection in a population which may ultimately have a bearing on the host biology (Merino et al. 2000), and has been widely used in studies of parasitism (Bennett et al. 1995, Deviche et al. 2001, 2005, Valera et al. 2006).

Differential leucocyte counts were determined by examining randomly selected and non-overlapping microscope fields of each smear at $1000 \times$ magnification under oil immersion and counting leucocytes until we reached a total of 100 cells. Eosinophils (E), heterophils (H), basophils, lymphocytes (L), and monocytes were identified according to the criteria of Campbell (1995). The heterophil/ lymphocyte (H:L) ratio was used as an index of chronic stress (Vleck 2000, Bonier et al. 2007) based on the observation that increased glucocorticoid secretion may result in lymphocytopenia and a subsequent increase in heterophil numbers (Harmon 1998). Moreover, the H:L ratio increases in response to a variety of "stressors" including malnutrition, water deprivation, and injury (Gross and Siegel 1986, Tripathi and Bhati 1997, Vleck et al. 2000). To determine repeatability of the leucocyte differential counts, 12 smears were analyzed three times each and Kendall's coefficient of concordance was used to compare leucocyte numbers (Siegel 1956). Counts were highly correlated for the three most abundant leucocyte types (H: $W = 0.901$, L: $W = 0.962$, and E: $W = 0.862$, all $P < 0.001$). Total leucocyte count (TLC) was also measured to estimate the overall allocation to leucocyte production. For this the number of leucocytes per 10,000 erythrocytes were counted using the same digitized images generated for measuring *Haemoproteus* density.

Statistical analysis

Body condition, a measure of stored energy reserves, was determined using the standardized residuals of a reduced major axis (RMA) regression of tarsus length on body mass for each species (Green 2001). Individuals with a greater amount of body mass for a given size are thought to have a greater amount of energy reserves and to be in better body condition (Green 2001). Body condition indices in birds often rely on ordinary least squares regression (OLS) of a linear morphometric measurement, such as tarsus length on body mass (Stevenson and Woods 2006). However, the use of OLS regression has recently been questioned in situations where both the independent and dependent variables are subject to error (Green 2001). Thus RMA regression residuals were used to account for error in the independent variable.

Comparison of parasite prevalence were done using hierarchical loglinear analysis, which tests for associations between categorical variables, in a manner similar to analysis of variance. Species, classifications, sites, and life history stages were used as independent factors (see Table 1 for descriptions). The relationships between parasite infection density (using only infected individuals), TLC, and body condition were assessed using Pearson correlations. Differences in leucocyte proportions were tested for normality with Kolmogorov-Smirnov tests. Non-normally distributed data were arcsine square root transformed and H:L ratios were log-transformed before analysis. Haematological variables and body condition were compared for each species using two-way analysis of variance (ANOVA) with locality, life history stage (pre-breeding, breeding, or post-breeding), and their interaction as factors. Post-hoc comparisons between sites were done with Tukey-Kramer honestly significant difference (HSD) tests. Multiple univariate comparisons ($n = 5$) of hematological variables necessitated the re-adjustment of alpha levels (Zaykin et al. 2002). A sequential Bonferroni correction was used to adjust this level to $P = 0.01$ and this is presented along with $P = 0.05$ for reader evaluation. Data are presented as means $\pm$ SE and were analyzed using SPSS 13.0.

Results

Body condition

Among urban and rural sites, body condition, did not differ for any species (although not all species were sampled in each locality), and thus samples were pooled into two groups (urban and rural) per species for analyses. Body condition did not differ between urban and rural sites for three species (ABTO: $F_{1, 55} = 0.95$, $P = 0.07$; CBTH: $F_{1, 44} = 0.12$, $P = 0.71$; HOSP: $F_{1, 45} = 1.07$, $P = 0.08$), but urban NOMO had higher body condition scores than their rural counterparts ($F_{1, 32} = 10.18$, $P = 0.01$).

Comparing life history stages, rural CBTH ($F_{1, 22} = 14.29$, $P = 0.02$), ABTO ($F_{1, 31} = 9.17$, $P < 0.05$), and CANT ($F_{1, 14} = 11.31$, $P = 0.033$) were in better condition during that after their breeding period (Fig. 1). Body condition did not vary with life history stage in NOMO ($F_{1, 32} = 0.70$, $P = 0.401$), or HOSP ($F_{1, 45} = 0.41$, $P = 0.328$). In no species were there differences in body condition between pre-breeders and breeders (all $P > 0.6$) or between pre-breeders and post-breeding birds (all $P > 0.8$; Fig. 1).

The interaction of locality and life history stage for CBTH was significant ($F_{1, 22} = 4.606$, $P = 0.033$), with pre-breeding rural birds being in better body condition than urban counterparts ($P = 0.049$; Fig. 1). This interaction was also significant for HOSP ($F_{1, 45} = 4.004$, $P = 0.048$) with urban post-breeding HOSP being in poorer condition than rural post-breeders ($P = 0.037$; Fig. 1). Other interactions
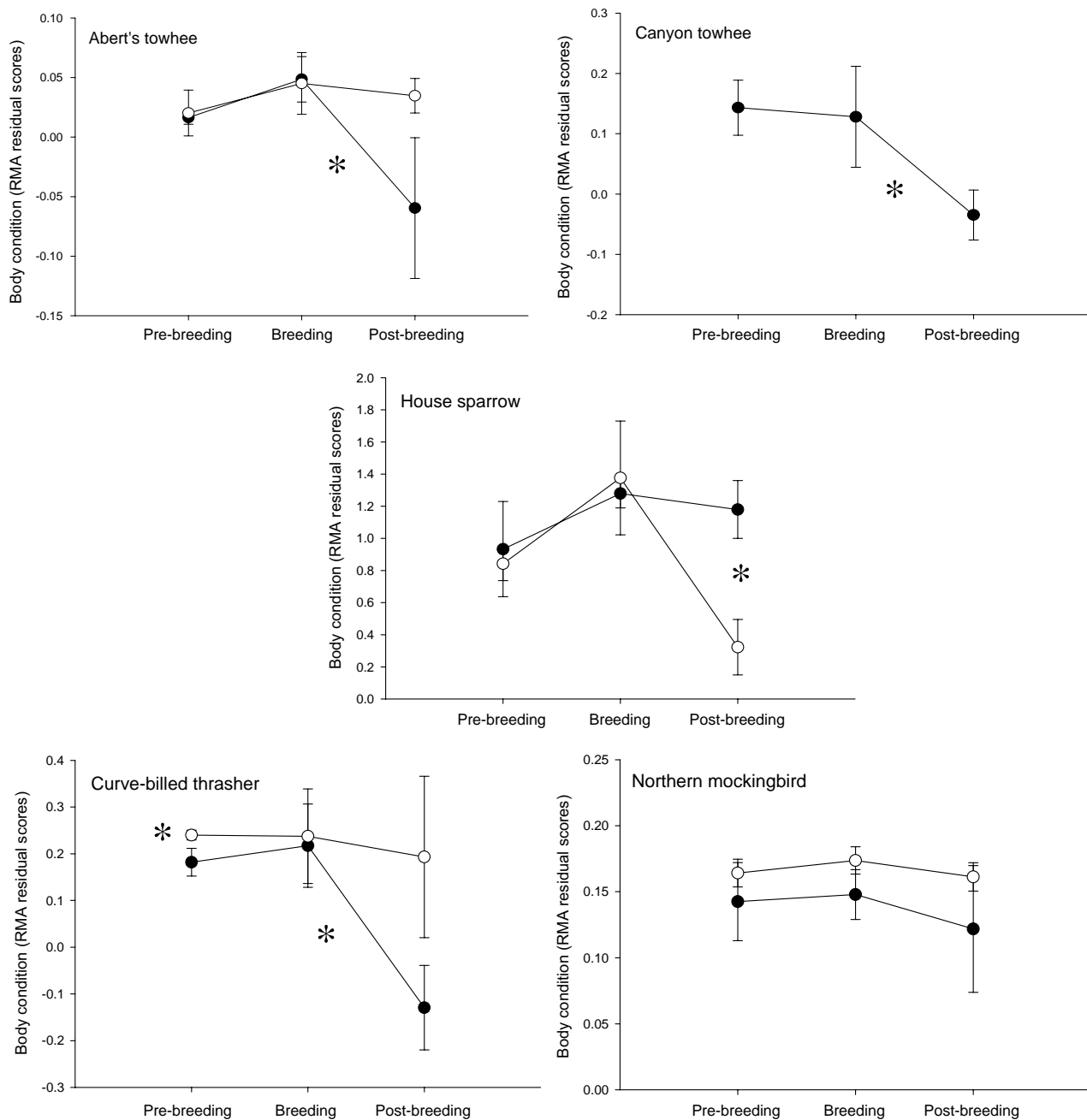
Figure 1. Changes in body condition with life history stage for five bird species inhabiting urban (open circles) and rural (filled circles) habitats in the Sonoran Desert region (only data for rural birds was available for one species). Body condition scores are based on residuals of a reduced major axis regression (RMA) of body mass (g) on tarsus length (mm). Asterisk indicates significant differences between points ($P \leq 0.05$). Sample sizes and median sampling dates are provided in Table 1.

between life history stage and locality were not significant (all $P > 0.09$).

Blood parasite types

We detected three parasite types: Microfilariae *Haemoproteus* and *Trypanosoma* (Table 2). *Haemoproteus* were identified as *H. fringillae* in CANT and *H. beckeri* in CBTH. Neither *Trypanosoma* nor microfilariae could be identified at the species level. All three parasite types were detected in CANT and CBTH (Table 2). Only micro-

filariae were detected in ABTO, and only *Haemoproteus* was detected in NOMO (Table 2). No parasites were detected in HOSP (Table 2).

Parasite prevalence

The prevalence of *Haemoproteus* ($\chi^2 = 17.93$, df = 4, $P < 0.001$), and microfilariae ($\chi^2 = 11.02$, df = 4, $P < 0.001$) was species-specific. *Trypanosoma* prevalence was low in CANT and CBTH (Table 2), and thus, was excluded from statistical analyses. Classification (Table 1)

Table 2. Summary of blood parasite prevalence between urban and rural populations for five Sonoran Desert bird species. See Table 1 for species abbreviations.

Species	Habitat	Sampling dates (2006)	n	Parasite prevalence (% infected birds)			
				Haemoproteus	Microfilariae	*Trypanosoma*	Overall
ABTO	Rural	Jan. 18 – Sept. 19	32	0	44	0	44
	Urban	Jan. 19 – Sept. 14	24	0	0	0	0
CANT	Rural	Apr. 29 – Sept. 4	15	80	53	7	100
NOMO	Rural	Jan. 18 – Sept. 10	10	0	0	0	0
	Urban	Jan. 13 – Aug. 22	23	22	0	0	22
CBTH	Rural	Jan. 28 – Sept. 19	23	30	9	4	39
	Urban	Jan. 29 – Sept. 7	22	18	9	0	23
HOSP	Rural	Febr. 5 – Aug. 4	17	0	0	0	0
	Urban	Jan. 30 – Sept. 12	29	0	0	0	0

did not influence prevalence of *Haemoproteus* and microfilariae (all P > 0.05).

No parasites were detected in urban ABTO, but microfilariae were detected in rural ABTO ($\chi^2 = 16.28$, df = 2, P = 0.014) and prevalence was higher in breeding than pre-breeding or post-breeding birds (ABTO × site × life-history stage: $\chi^2 = 9.47$, df = 3, P = 0.015). CANT were infected with microfilariae and *Trypanosoma* only during the breeding season (Fig. 2), but *Haemoproteus* prevalence was lower during the breeding season than before or after it (CANT × site × life-history stage: $\chi^2 = 14.44$, df = 3, P = 0.039).

Parasite prevalence did not differ between urban and rural populations of CBTH (*Haemoproteus*: $\chi^2 = 2.21$, df = 2, P = 0.315; microfilariae: $\chi^2 = 1.61$, df = 2, P = 0.630). In urban CBTH, *Haemoproteus* prevalence was higher in pre-breeding birds than during the breeding or post-breeding periods (CBTH × site × life-history stage: $\chi^2 = 11.74$ df = 2, P = 0.01). In rural CBTH, *Haemoproteus* prevalence did not differ between pre-breeding and breeding birds, but differed from post-breeding (CBTH × site × life-history stage: $\chi^2 = 11.10$, df = 3, P = 0.023). No difference in *Haemoproteus* infection with life-history stage was detected for NOMO (NOMO × site × life-history stage: $\chi^2 = 0.71$, df = 3, P = 0.48).
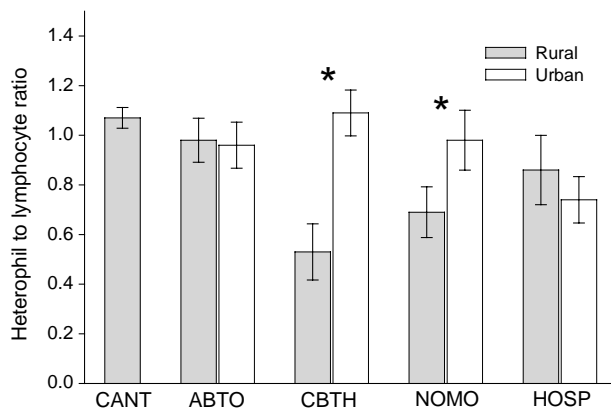

Figure 2. Differences in the ratio of heterophils to lymphocytes between urban and rural populations in five species of Sonoran Desert birds between urban and rural populations. Species codes are defined in Table 1.

Correlations with parasite density

Microfilariae density was not correlated with body condition in any species regardless of site, locality or life history stage (r = −0.19 to −0.08, all P > 0.1). There was a negative correlation between body condition and *Haemoproteus* infection density in CANT (r = −0.31, P = 0.004), but not in CBTH (r = −0.13, P = 0.091), or NOMO (r = −0.09, P = 0.39). Infection with multiple parasite types was not associated with body condition in CANT ($F_{1, 14} = 0.24$, P = 0.18). The number of CBTH that had multiple parasite infections was insufficient to test this relationship. Non-parasitized urban CBTH did not differ in body condition scores from parasite-free rural counterparts (*t*-test = 0.73, P = 0.063).

Leucocyte characteristics

Haematological parameters are summarized in Table 3. Lymphocytes were the most abundant leucocytes in all species except in CANT and urban CBTH, where heterophils were most common (Table 3). In all species basophils and monocytes represented only a small component of the total leucocyte count and thus statistical analyses of these were omitted due to a lack of statistical power.

No differences in H:L ratio were observed between urban and rural ABTO (Table 4), or between ABTO and its congener, CANT ($F_{1, 41} = 1.181$, P = 0.285; Fig. 2). However, more eosinophils were present in CANT than in ABTO blood ($F_{1, 41} = 14.73$, P = 0.008). Urban CBTH and NOMO had higher H:L ratios than rural birds (Fig. 2) resulting from significant increases in heterophils and decreases in lymphocytes (Table 3). Urban CBTH and NOMO also had higher percentages of eosinophils than rural birds (Table 4). Rural NOMO and CBTH had a lower TLC than urban conspecifics, but TLC did not differ between localities for the other species (Table 4). Urban and rural HOSP did not differ with respect to their H:L ratios (Fig. 2), but rural HOSP had more eosinophils than urban birds (Table 4).

Correlations with haematology

Body condition was not correlated with any hematological characteristic in any species (all P > 0.06). For the three species that could be tested, infection with blood parasites

Table 3. Mean proportions of heterophils (H), lymphocytes (L) eosinophils (E), basophils (B), monocytes (M), ratio of heterophils to lymphocytes (H:L), and total leucocyte counts (TLC) for five species of Sonoran desert birds in both urban and rural habitats. Numbers in parentheses indicate SE. See Table 1 for species abbreviations, and Table 2 for sample sizes.

Species	Habitat	Percent H	Percent L	Percent E	Percent B	Percent M	H:L	TLC
ABTO	Rural	39.8 (1.8)	51.3 (2.0)	7.5 (0.9)	0.6 (0.2)	1.4 (0.2)	0.91 (0.13)	60.0 (7.9)
	Urban	43.5 (2.2)	50.0 (2.4)	4.9 (0.7)	0.2 (0.1)	1.3 (0.4)	0.93 (0.10)	41.2 (6.1)
CANT	Rural	46.3 (2.5)	33.1 (1.5)	12.8 (0.4)	0.8 (3.6)	7.3 (0.3)	1.70 (0.74)	42.3 (3.2)
NOMO	Rural	26.3 (4.0)	72.5 (3.1)	1.5 (0.5)	0.3 (0.1)	0.5 (0.2)	0.61 (0.16)	19.0 (7.0)
	Urban	40.6 (2.5)	49.3 (2.7)	8.6 (1.2)	0.5 (0.2)	1.1 (0.2)	0.92 (0.10)	35.2 (3.9)
CBTH	Rural	31.5 (1.6)	55.8 (2.7)	9.6 (1.5)	0.6 (0.3)	2.5 (0.8)	0.62 (0.06)	67.3 (7.7)
	Urban	45.8 (2.8)	41.4 (3.9)	12.3 (2.3)	0.3 (0.2)	1.5 (0.9)	1.34 (0.21)	53.7 (7.6)
HOSP	Rural	39.1 (3.7)	51.3 (2.9)	7.5 (4.3)	0.6 (0.3)	1.5 (0.4)	0.83 (0.11)	38.2 (8.1)
	Urban	38.4 (9.7)	56.7 (7.5)	2.6 (1.8)	0.2 (0.1)	2.0 (0.4)	0.79 (0.14)	44.5 (10.3)

was associated with elevated H:L ratios (Fig. 3; ABTO: t-test $=2.77$, $P=0.016$; CBTH: t-test $=2.16$, $P=0.032$; NOMO: t-test $=2.11$, $P=0.047$), and TLC in CBTH (t-test $=3.13$, $P=0.003$), and ABTO (t-test $=2.71$, $P=0.011$). When comparing localities, we found urban *Haemoproteus*-infected CBTH to have lower TLC (t-test $=4.14$, $P=0.02$), and a smaller H:L ratio (t-test $=3.81$, $P=0.007$) than their rural counterparts. However, there were no such differences between urban and rural CBTH parasitized with microfilariae (all $P>0.6$).

Discussion

Interspecific patterns of blood parasitism

We examined microgeographic variation in blood parasites and leucocyte profiles in sedentary Sonoran Desert bird species in urban and rural areas around Phoenix to test the hypothesis that urban-adaptable species exhibit lower parasitism, better body condition, and a greater immune capacity in urban than rural areas. Urban birds typically had lower parasite prevalence than rural birds, but this difference was not consistent across species. We observed large species-specific differences in parasite infections between closely related species inhabiting similar habitats. A study of *Aimophila* sparrows in the Sonoran Desert also found large differences between species inhabiting similar habitats and localities, which may be associated with differences in nest site selection (Deviche et al. 2005). Collectively, these observations suggest that haemoparasitism is not necessarily uncommon in arid environments as has been previously suggested (Bennett et al. 1992, Little and Earle 1995, Tella et al. 1999, Valera et al. 2003). Additionally, interspecific differences in haemoparasitism suggest that differences in vector abundance between

habitats do not solely account for patterns of haemoparasitism.

Are urban areas sources of blood parasite vectors?

We predicted that increased presence of standing water within city limits would increase dipteran vector numbers or diversity which would subsequently increase infection exposure in urban birds. Lower microfilariae prevalence in urban than rural birds may be associated with a lack of habitat for the biting midges (Ceratopogonidae: *Culicoides* spp.), its potential predominant vector in the Southwest US (Wirth and Hubert 1960). In the arid southwestern United States the larval stage of some *Culicoides* spp. depends on moisture derived from decaying parts of cacti (Wirth and Hubert 1960, Blanton and Wirth 1979) and the lesser abundance of decaying cacti within Phoenix as compared to rural habitats may restrict the presence of this vector in urban areas. Infection with *Haemoproteus* did not vary with urbanization in CBTH, supporting the idea that CBTH presence in Phoenix may be associated with only peripheral colonization of the city or that the vector for *Haemoproteus* may occur within these areas of the city. Investigations on variation in dipteran vector abundance across urban-rural gradients are warranted.

Differences in parasite infections between populations may result from numerous ecological factors including differences in distributions of parasite-transmitting vectors and subsequent host exposure (Atkinson and Van Riper III 1991, Shurulinkov and Chakarov 2006), or the lack of spatial overlap between host and vectors (Atkinson and Van Riper III 1991). Physiological differences in host's ability to resist infection (Lindström and Lundström 2000, Yorinks and Atkinson 2000), variation in host mortality (Merino et al. 2000), or levels of sociality (Barnard et al. 1998,

Table 4. Differences in proportions of three leucocytes, the ratio of heterophils to lymphocytes (H:L), and the total leucocyte count (TLC) across an urban-rural gradient for four species of Sonoran desert birds. See Table 1 for species abbreviations and Table 2 for sample sizes.

	ABTO		CBTH		NOMO		HOSP	
	$F_{1,55}$	P	$F_{1,44}$	P	$F_{1,32}$	P	$F_{1,45}$	P
Percent Heterophils	2.23	0.12	9.38	<0.001**	0.09	0.03*	0.31	0.57
Percent Lymphocytes	1.38	0.41	2.57	0.013*	4.14	<0.001**	0.23	0.84
Percent Eosinophils	0.94	0.071	7.14	0.011*	3.84	0.004**	6.19	0.036*
H:L ratio	0.22	0.645	46.50	<0.001**	18.1	<0.001**	0.56	0.480
TLC	1.03	0.078	1.65	0.042*	2.74	0.039*	0.49	0.41

*significant at $P<0.05$. **significant after Bonferroni-corrected alpha $P<0.01$.
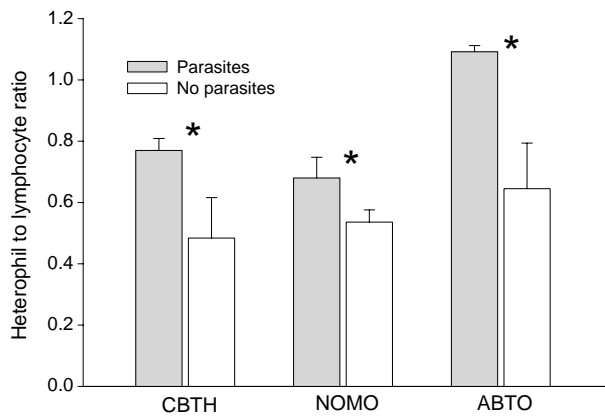
Figure 3. Relationship between blood parasite infection and the ratio of heterophils to lymphocytes for three Sonoran Desert bird species. Species codes are defined in Table 1.

Adriano and Cordeiro 2001), may also alter patterns of parasite infection. Arizona HOSP are primarily associated with urbanized and agricultural areas, which are typically mesic habitats with relatively abundant supplies of water. Additionally, unlike the other species examined in our study, HOSP are gregarious and this would be expected to augment transmission of parasites, through the infection of mutliple hosts by vectors. The lack of parasitism in HOSP, an urban-specialist, contrasts with prevalence estimates from Russia (34%, Valkiunas et al. 2006) and the eastern USA (29%, Lee et al. 2006). This may reflect strong resistance to infection, a lack of specialization to HOSP on the part of the vector, or perhaps a high rate of mortality associated with infection. Geographic variation in the immune response has been studied in HOSP (Martin et al. 2004). In this species, individuals from temperate regions exhibit a stronger response to phytohemaglutinin challenge than tropical birds and a ''common garden'' study suggests that this difference does not entirely result from acclimation (Martin et al. 2004). Further studies on microgeographic variation in immune responsiveness and susceptibility will shed light on how the urban environment may influence patterns of parasitism.

Blood parasitism and body condition as a function of life history stage

Most species had lowest body condition after breeding and this was most pronounced for rural ABTO and CBTH. However, this difference was decreased in urban birds, which may be associated with more constant resource availability in urban environments. Although post-breeding rural ABTO had the lowest body condition scores, rural ABTO in breeding condition had the highest prevalence of microfilariae. Similarly, haemoparasites were not detected in post-breeding rural CBTH, but they were detected before and during breeding. Enhanced blood parasitemia in breeding condition birds may result from effects of elevated reproductive hormones. Indeed, these hormones can cause a relapse of existing infections and increase the susceptibility to new infections (Deviche and Parris 2006). In addition, timing of breeding in desert birds is often closely associated with rainfall patterns (Deviche and Small 2005, Small et al.

2007), which also determine the patterns of emergence of many dipteran vectors (Wirth and Hubert 1960).

Blood parasites and immune capacity

Differences in parasite intensity and prevalence between populations may be related to differences in immunity and clearance rates (Palacios and Martin 2006). We found that parasitism was associated with elevated H:L ratios in three species, and urban CBTH infected with *Haemoproteus* had lower TLC and higher H:L ratios than their rural counterparts. Collectively, these observations suggest an energetic cost associated with fighting infection which differs between urban and rural populations of birds. Bonier et al. (2007) reported increased investment into immunity by breeding female white-crowned sparrows *Zonotrichia leucophrys*, and in turn a fitness cost measured as decreased fledging success associated with blood parasitism. However, haemoparasitism is typically thought to be associated with decreases in H:L ratio because lymphocytes are thought to proliferate in response to parasitic infection (Fudge 1989). In contrast, heterophils are thought to be upregulated during bacterial infection (Fudge 1989, Harmon 1998). One possible explanation for the increased H:L ratio in parasitized birds is that haemoparasitic infections are associated with decreased resistance to other forms of infection (e.g. bacterial) that promote heterophilia (Harmon 1998). The increases in H:L ratio in our study may also be associated with chronically increased circulating levels of glucocorticoids, which can be immunosuppressive (Oppliger et al. 1998, Sapolsky 2000, French et al. 2006), and may differ between urban and rural bird populations (Schoech et al. 2004, Partecke et al. 2006, Bonier et al. 2007).

Resource availability, body condition, and immune function

Trade-offs between life history components and immunocompetence are thought to be paramount under conditions of limited resources (Sheldon and Verhulst 1996, Wiehn and Korpimäki 1998). Urban areas have been characterized as seasonally buffered with respect to temporal availability of resources, and this has been suggested to provide an increased opportunity for breeding (Schoech and Bowman 2001, Partecke et al. 2005). Urban birds that are better capable of exploiting food resources may allocate energy to immunity without compromising reproductive effort. Thus urban-adaptable species (ABTO, NOMO, and HOSP) that are infected with blood parasites would be predicted to exhibit a greater increase in leucocyte numbers in urban than rural areas and this may be reflected in urban birds having higher body condition scores than rural birds.

Urban CBTH had a higher leucocyte count and H:L ratio than rural birds, but when considering the effects of parasitic infection, urban CBTH had smaller TLC and H:L ratios than parasitized rural birds. However, this difference did not appear to result from urban CBTH being in better body condition than rural birds. Understanding how species differentially use anthropogenic resources may offer insight into the patterns of body condition and immune function capacity.

Research has begun to focus on how anthropogenic disturbance influences the physiology of animals (Partecke et al. 2006). Such studies may help understand how multiple elements of a novel environment interact to modify selection pressures acting at the organismal level. Shifts in behavioral traits and physiological parameters in response to urbanization can only be identified by testing specific components of the urban landscape and its direct effects on wildlife.

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