Behavioral Ecology
doi:10.1093/beheco/ari044
Advance Access publication 13 April 2005

A taste for novelty in invading house sparrows, *Passer domesticus*

Lynn B. Martin II and Lisa Fitzgerald
Department of Ecology and Evolutionary Biology, Princeton University, Princeton NJ 08544, USA

One of the central questions in invasion biology involves why some introductions succeed and others fail. Although several correlates of invasion success have been identified, patterns alone cannot identify the mechanisms underlying the invasion process. Here, we test the hypothesis that one predictor of invasion success, behavioral flexibility, is different between invading and established populations of the same species of bird. We predicted that neophobia (fear of novelty), a surrogate of behavioral flexibility, would be weaker in an actively invading population (28 years resident; Colon, Republic of Panama) of house sparrows (*Passer domesticus*) compared to a population that had been resident for more than 150 years (Princeton, New Jersey, USA). To test this hypothesis, we compared latency to consume novel foods and phobia of novel objects between populations when both were kept under similar environmental conditions in captivity. As predicted, birds from the 150-year-old population took significantly longer to approach and consume novel foods than birds from the 28-year-old population. Responses to novel objects were not different between populations however; both populations fed more readily near some novel objects, which to our knowledge is the first such occurrence in a wild vertebrate species. Overall, a predilection for trying new foods and being attracted to novel objects may in part explain how this species has so successfully invaded new areas. *Key words:* foraging, invasive species, neophobia, range expansion. *[Behav Ecol 16:702–707 (2005)]*

Organisms confront many challenges when moving into new areas. To become established, introduced animals must quickly and accurately identify food, shelter, and breeding sites, and they must recognize potential predators and competitors (Coleman and Mellgren, 1994). To date, many correlates of invasion success have been identified, including size (Cassey, 2001; Thebaud and Simberloff, 2001); reproductive effort (Green, 1997); disposition to migration (Veltman et al., 1996); sexual dimorphism (McClain et al., 1999; Sorci et al., 1998); immune defense (Lee and Klasing, 2004); breeding site choosiness and diet (Newsome and Noble, 1986); the size, number, and demographic composition of introduced propagules (Duncan et al., 2003; Legendre et al., 1999; Viet and Lewis, 1996); and the community into which introductions are made (Lodge, 1993). Although these studies indicate that the invasion process is at least in part deterministic (Duncan et al., 2003), none identify specific mechanisms by which successful invaders establish and expand their new ranges (Ehrlich, 1989; Mack et al., 2000; Viet and Lewis, 1996). Even large demographically balanced introductions sometimes fail (Lever, 1987; Long, 1981). During range expansions, a lag phase often precedes rapid population growth (Sakai et al., 2001; Viet and Lewis, 1996).

Recently, behavioral flexibility was identified as a potentially important mechanism by which avian invasions could progress (Sol and Lefebvre, 2000; Sol et al., 2002). Increased behavioral flexibility could allow individuals to colonize new areas because they would readily recognize and hence utilize unfamiliar resources (Greenberg, 1990; Mayr, 1965; Webster and Lefebvre, 2001). Two aspects of behavioral flexibility include (1) propensity to consume unfamiliar foods and (2) responsiveness to novelty (Greenberg, 1984, 1990a,b; Greenberg and Mettke-Hofmann, 2001; Murphy, 1978). Generally, one would predict that behaviorally flexible species would be more willing to explore particular objects or situations that neophobic species might avoid (Greenberg and Mettke-Hofmann, 2001) and more willing to consume potential food resources in general (Sol et al., 2002). Food preference in particular should be closely connected to invasion status because a population "that readily tastes new foods or adopts novel foraging strategies (should be) more pre-adapted to survive and reproduce in a novel environment than a more specialized (population) that persists with the behaviors of its area of origin" (Sol et al., 2002). To date, ample evidence indicates that vertebrate species, including humans, exhibit variation in motivation to seek out (or avoid) novel situations or foods (Bolivar and Flaherty, 2004; Cowan, 1977; Greenberg, 1990b; Haemig, 1989; Heinrich et al., 1995; Mitchell, 1976; Pliner et al., 1993). In multiple taxa, object neophobia has a genetic component (Bolivar and Flaherty, 2004; Minvielle et al., 2002).

Here, we tested whether an actively invading population of birds was less fearful of novelty and more willing to consume novel foods than an established population of the same species (Mayr, 1965). Indeed, animals can respond to novelty in at least three different ways: they can be attracted to it (neophilia), repulsed by it (neophobia), or indifferent of it. To test our hypotheses, we compared latency to approach and eat novel foods and latency to eat and approach familiar food in the presence of novel objects between two populations of house sparrows (*Passer domesticus*). We expected that sparrows invading the city of Colon, Panama, would more readily feed on seed near novel objects and would be quicker to consume novel foods than those from Princeton, New Jersey, USA. The latter population has been resident for more than 150 years (Long, 1981; Summers-Smith, 1988), while the former is still actively spreading across the country (Ridgely and Gwynne, 1989). To ensure that our results were not an artifact of differential resource availability or diversity, interspecific competition, or predation pressure between sites, we conducted our study on animals kept under controlled conditions in captivity. Also, to account for potential demographic

---

Address correspondence to L. Martin, who is now at the Department of Psychology, Townshend Hall, Ohio State University, Columbus OH 43210, USA. E-mail: lmartin@mail.psy.ohio-state.edu.

Received 7 December 2004; revised 26 February 2005; accepted 8 March 2005.

variability of populations (Greenberg, 1983; Heinrich et al., 1995; Marchetti and Price, 1989; Murphy, 1978), we held all birds in captivity for 8 months prior to experiments.

METHODS

Study species

The house sparrow was introduced to multiple locations in North America from Europe in the 1850s (Long, 1981). Since then, the species has spread north as far as Alaska and south as far as Panama (Long, 1981; Ridgely and Gwynne, 1989; Summers-Smith, 1988). Across this introduced range, house sparrow populations show extensive morphological and physiological differentiation (Johnston and Selander, 1964; Kendeigh, 1976; Martin et al., 2004, 2005; Summers-Smith, 1988), yet within this area and worldwide, the species remains a strong commensal of humans. The successful and rapid colonization of this species has been attributed to multiple factors including the larger brain size, greater number of behavioral innovations, and tendency towards human commensalism (Sol et al., 2002; Summers-Smith, 1988). The house sparrow has not enjoyed as much success in its invasion of the Neotropics as it has in other parts of the world (Summers-Smith, 1988); currently, the factors reducing the rate of expansion of populations near the equator in the Western hemisphere are unknown (Long, 1981).

The diet of North American house sparrows is predominantly plant matter (80–90%; Weins and Dyer, 1977). Of this vegetation, 40–75% is seeds. The remainder of the diet consists of flowers, buds, leaves, insects, and a broad array of human refuse (Summers-Smith, 1988). In Europe, diet composition is generally similar to that in North America (Weins and Dyer, 1977). In fact, the most dramatic differences in diet between populations occur within a relatively small range. Typically, rural populations consume human-produced cereal grains, whereas urban populations ingest human food waste (Summers-Smith, 1988). Consumption of insects and animal matter is usually limited to spring and summer, and then only constitute 15–20% of the diet. To date, the diets of wild birds in this study have not been characterized. We expect that human refuse constitutes a large part of the diet of both populations in this study because both live in relatively urbanized habitats.

Bird capture and care

In November 2002, birds were captured in mist nets from Colon, Panama (9° 1′ N, 80° 1′ W). Soon after, birds were transported to Princeton, New Jersey, USA (40° 21′ N, 74° 40′ W) where, after a 30-day quarantine period, they were kept with another group of sparrows caught locally (from an open-air shopping mall) in climate-controlled, free-flight aviaries. For 8 months thereafter, all birds were held under similar environmental conditions (ambient temperature and relative humidity) and allowed to breed (in the nest-boxes provided). Diet while in captivity consisted of Kaytee Supreme© seed mix (Chilton, Wisconsin, USA), sliced oranges, boiled mashed chicken eggs, live mealworms (*Tenebrio molitor*; Fluker Farms, Port Allen, Louisiana, USA), fresh spinach, dried insect larvae (Bag O' Bugs; Golden West Bird Products, Mission Hills, California, USA) and vitamin supplements (Daily Supplement 3; Golden West Bird Products). For the duration of captivity and experimentation, the photoperiod was maintained 14:10 light:dark. In all experiments, only mature animals were used, and a similar number of males and females were included in all trials.

Novel food consumption

In July 2003, we conducted novel food consumption experiments. The night before each trial, birds were captured from aviaries and weighed. Then, molt (1–3, 3 being heaviest) and fat (1–5, 5 being the highest score) were scored. Birds were then kept overnight (and for the duration of the trial, 2 days) in individual cages (16″ × 13.5″ × 15.5″), visually isolated from one another. In other taxa, feeding on novel foods is increased if animals see conspecifics consume novel foods (Visalberghi and Addessi, 2000). The next morning (0700 h) after a 14-h nocturnal (fasting) period (Greenberg and Mettke-Hofmann, 2001) each bird was given an equal mass of either a novel food or seed (Kaytee Supreme©, Chilton), the major constituent of their diet in captivity prior to the experiment.

The novel foods were (1) a dollop of chunky peanut butter, (2) slices of kiwi fruit, (3) finely crushed, artificially fruit-flavored hard candy (LifeSavers$^{\text{TM}}$), or (4) a mixture of strained, boiled yogurt, hardboiled chicken eggs, canned dog food, and breadcrumbs (modified from a diet used for hand-reared nestling birds by Gwinner et al., 1988). We chose these four foods to maximize texture, color, smell, and flavor diversity so that each treatment was both new and surprising relative to the typical seed diet (Heinrich et al., 1995; Immelmann and Beer, 1989). The cups in which food was provided were always identical, and they were placed so that their contents could be seen from any position within the cage.

As soon as foods were distributed among cages, we monitored and video recorded behavior from an observation blind. For each animal, latency to approach food (within pecking distance, <10 cm) and latency to consume food (active pecking) were recorded. After 3 h of continuous observation, food was removed from the cages and weighed to the nearest 0.01 g. If birds had not approached/consumed food by the end of this period, they were given a maximal score of 12,000 s; videos were then reviewed to be sure that latency measures were accurate. After each trial, birds were given seed to sustain them for the rest of the day. At the end of the lights-on period (1700 h), this seed was removed. A second trial, identical to the first except for the type of food given to birds, was conducted the next day. The order of treatments (novel food versus seed [controls]) was assigned randomly on the first day of each trial; birds received the alternate food type the next day. Eight birds from each population were used for each food type ($N_{\text{total}} = 64$).

Phobia of novel objects

To compare object neophobia between populations, a second experiment using a similar protocol and the same individuals as in the prior experiment was conducted (Greenberg, 1983, 1990a,b). The first morning after capture from aviaries, latency to feed/approach seed-filled cups in the absence (control) and presence (treatment) of one of four novel objects was recorded for each bird, again from behind a blind (Greenberg, 1990a; Webster and Lefebvre, 2001). The four novel objects in this experiment were colored ribbon, a plastic toy lizard, a rubber ball, and a colored food cup that had been used to feed other birds in separate experiments; each was placed immediately next to food dishes during trials. As above, we chose the particular novel objects to maximize their diversity, but only one at a time (randomly chosen) was placed next to a food cup. Besides this difference, the experimental protocol was identical to the above food neophobia procedure. As for the food neophobia trials, eight birds per object were used from each population ($N_{\text{total}} = 64$).

Data analysis

Prior to analysis, the control measures for each bird (food preference: approach and feed latencies for seed; object neophobia: approach and feed latencies when no object nearby) were subtracted from the latencies of the same birds when novel foods or objects were present. This allowed us to compare behavior irrespective of activity level or motivation among individuals. Crushed hard candy was not consumed by either population; latency data from these trials were therefore removed from analysis.

After the above transformations, we determined if data met the assumptions of parametric statistics using one-sample Kolmogorov-Smirnov tests and histograms. For parametrically distributed data, independent samples *t* tests or general linear ANOVA models (with simultaneous Bonferroni post hoc tests) with latency as the dependent variable and sparrow population and food type as fixed factors were used. For nonparametric and discrete variables (mass change, molt score, and fat score), Mann-Whitney *U* tests were used. For all analyses, we used SPSS v10, setting $\alpha = 0.05$.

RESULTS

Food neophobia

Invading house sparrows ($n = 24$), which were significantly smaller ($t_{46} = 4.88$, $p < .001$), approached ($F_{1,48} = 4.56$, $p = .038$) and consumed ($F_{1,48} = 5.75$, $p = .021$) novel food more readily than established birds ($n = 24$; Figure 1). We detected no significant interactions between food type and sparrow population however. Fat score prior to trials and mass loss during trials were also not different between populations (fat: $U = 401.5$, $p = .104$; mass loss: $U = 484.5$, $p = .712$), indicating that birds were in similar condition before and during trials. Established birds were molting more than introduced birds however ($U = 362.0$, $p = .032$). Lastly, some foods were preferred over others (Figure 2: $F_{5,48} = 12.28$, $p < .001$; food type $F_{2,48} = 30.14$, $p < .001$), but not in one population more so than another (origin: $F_{1,48} = .47$, $p = .496$). For three foods, a detectable amount was consumed (Figure 2). Crushed hard candy on the other hand was not consumed by either population and was therefore not included in latency analyses.

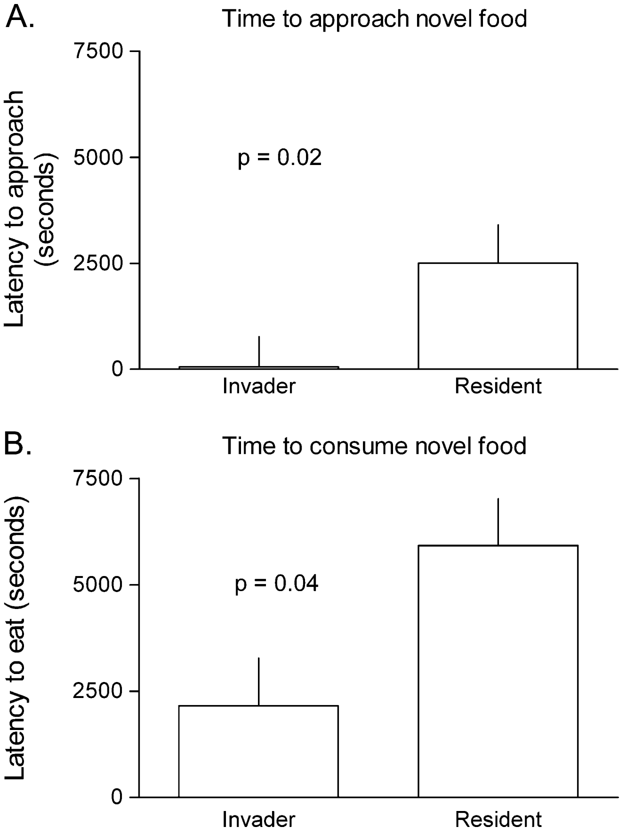

Figure 1
Latency to consumer (A) approach and (B) consume novel foods is significantly reduced in an invading (Panama) versus established (New Jersey) population of house sparrows. Bars represent means ± 1SE; *p* values from ANOVA.

Object neophobia

Neither latency to approach ($F_{7,64} = 1.95$, $p = 0.08$), nor latency to eat ($F_{7,64} = 1.26$ $p = .288$), nor any interaction terms varied significantly between sparrow populations ($n = 32$ for each population; Figure 3). In both populations, however, approach latency was affected by object type ($F_{3,64} = 3.88$, $p = .013$). Sparrows were more willing to approach seed-filled dishes when a ball or lizard or cup was nearby (Figure 4). Because this indicated that only the cup and ribbon were aversive, we compared neophobia between populations using only these two objects. Latency to approach ($t_{30} = 1.313$, $p = .20$) and feed ($t_{30} = 0.176$, $p = .861$) when objects were nearby were still not significantly different between populations.

DISCUSSION

Invasive species pose a large and growing threat to conservation of native and/or endemic species (Williamson, 1996), but little is known about the mechanisms underlying successful introductions and range expansions of invaders (Duncan et al., 2003; Mack et al., 2000). Behavioral plasticity is a strong predictor of invasion success among species (Sol and Lefebvre, 2000; Sol et al., 2002). Here, we provide the first experimental evidence that behavioral plasticity may be an important mechanism mediating the invasion process. We found that house sparrows from an actively invading population

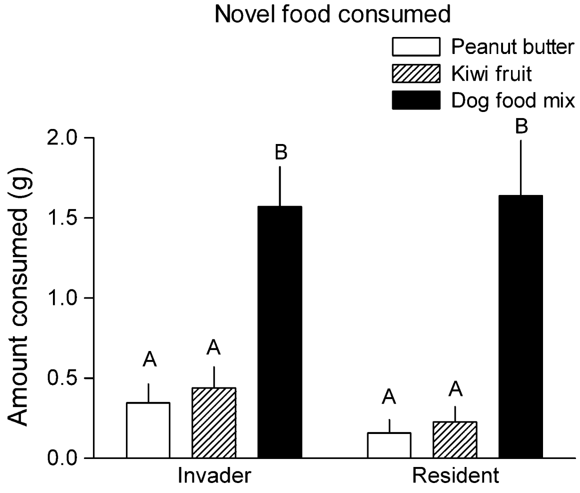

Figure 2
Consumption of dog food–yogurt mixture by house sparrows significantly greater than other novel foods. Bars represent means ± 1SE; letters indicate group membership by simultaneous Bonferroni post hoc test.

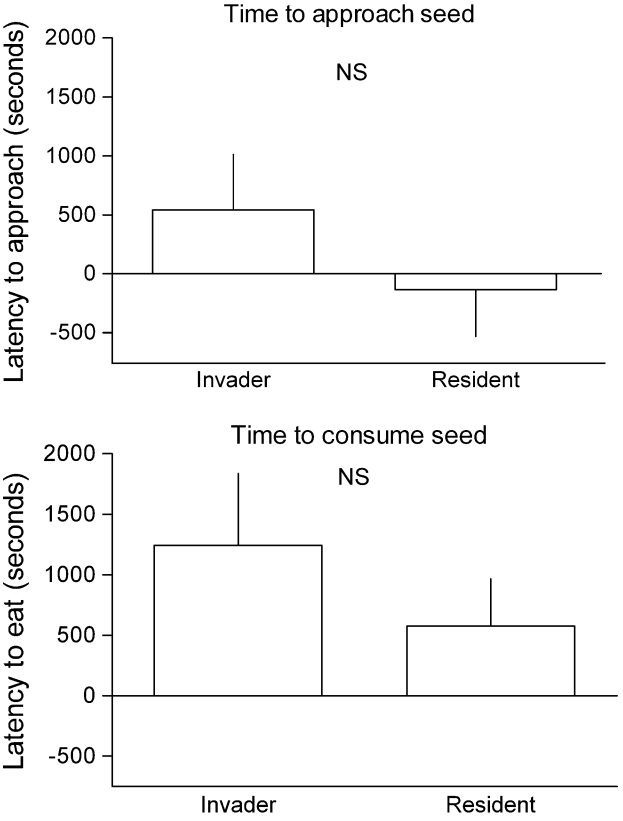

Figure 3
Fear of novel objects is not significantly different between established and invading house sparrows. No difference in (A) approach or (B) feed latency between populations when novel objects placed beside food dishes. Bars represent means ± 1SE; NS indicates no significant difference by ANOVA.

more readily approached and consumed novel foods than house sparrows from a population established more than 150 years ago, even when both were kept under common garden conditions for 8 months prior to study.

Why are some animals neophobic?

Exploration of novelty takes time and resources and may impose great risks (Greenberg and Mettke-Hofmann, 2001). On average, it may be more economical for animals to use resources that are familiar, particularly if they are specialized to certain types of prey (Beissinger et al., 1994). A strategy of seeking out and sampling alternative food or shelter may only be advantageous when (1) much of the environment is unfamiliar (Sol and Lefebvre, 2000) or (2) if preferred resources are depleted or rare (Beissinger et al., 1994; Pulliam, 1986). In the case of these house sparrow populations, the first alternative is likely the most important.

As the house sparrow has expanded its range, individuals have probably encountered a variety of food items, including native seeds, fruits, and insects, which were never experienced in the past. To persist in new areas, sparrows must have been forced to consume new food types. Those individuals that did so probably passed this predilection on to their offspring. What remains to be clarified though is why house sparrows from New Jersey lost this predilection to consume novel foods. Presumably, if reduced food neophobia is an important mechanism underlying the invasion process, the ancestors of New Jersey house sparrows would have also needed to be unafraid to sample new foods when they were initially introduced. Perhaps New Jersey sparrows have become specialized to the food available in their new range. One way to test this hypothesis involves replications of our experiments on house sparrows in their native range. We expect that Eurasian house sparrows would be more reluctant to sample novel foods than either population studied here.

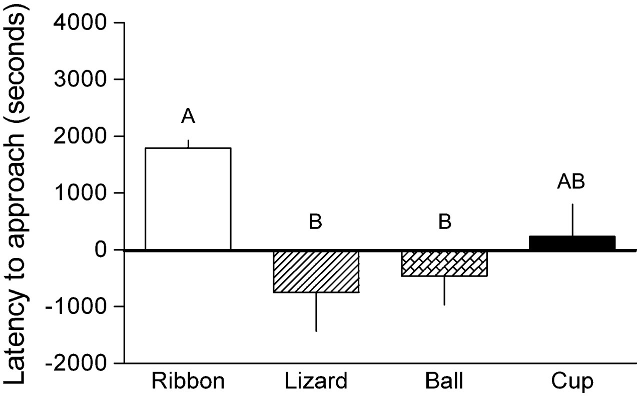

Figure 4
Certain novel objects are more aversive/attractive than others to house sparrows in object neophobia trials. Latency to feed when ribbon nearby significantly greater than toy lizard and rubber ball. Bars represent means ± 1SE; letters indicate group membership by simultaneous Bonferroni post hoc tests.

One other explanation why our sparrow populations differed in feeding neophobia involves the inherent dangers of the unfamiliar. For instance, some warbler species have been found to avoid habitats that are unfamiliar to them as a way to avoid potential predation (Greenberg, 1984). Likewise, some birds may favor familiar foods to avoid the toxins or disease-causing organisms that may be present in novel forms (Greenberg and Mettke-Hofmann, 2001). This possibility may be important for our New Jersey sparrows in particular as they were found to invest less in immune defense than their Panamanian counterparts (Martin et al., 2004). Indeed, immune defenses have recently been suggested to be important mediators of species' invasiveness (Lee and Klasing, 2004; Lee et al., in press). Defenses may also be related to the differential danger of consuming novel food sources across latitudes. One way to address this possibility would be to compare responses of each population to decomposing food.

One surprising finding in our study was that both populations were apparently attracted to two novel objects: the rubber ball and plastic lizard. Latency to approach food was shorter when these objects were placed next to food dishes. To our knowledge, this is the first record for novel objects being attractive to a vertebrate species; typically, vertebrates are either fearful or indifferent of novelty. Such a predilection for seeking out novelty may add to the list of characters (e.g., brain size, number of behavioral innovations) that make house sparrows generally better invaders than many of their relatives. Indeed, of 39 known introduction of house sparrows, 33 have been successful (Sol et al., 2002).

Why else might food preferences vary between populations?

Invading sparrows approached and consumed novel foods more readily than long-term resident sparrows, but our study cannot rule out that other factors have important influences on this pattern. For instance, food may be more diverse and/or less abundant in the tropics. One subspecies of scrub jays (*Aphelocoma insularis*) living on islands (where diet was purportedly more restricted) responded more favorably to novelty than another scrub jay subspecies (*Aphelocoma californica*) residing on the mainland (Haemig, 1989). Alternatively, differences in environmental conditions after or during ontogeny may have influenced foraging behavior between sparrow populations (Greenberg, 1990b; Mettke-Hofmann et al., 2002; Minvielle et al., 2002). For instance, the behavioral responses of pumpkinseed sunfish (*Lepomis gibbosus*) towards novel objects vary based on perceived predation risk (Coleman and Wilson, 1998). Likewise, social environment, particularly whether an individual can observe a conspecific eating a novel food, affects responsiveness towards novel foods in primates (Galef, 1993; Yamamoto and de Araújo Lopes, 2004).

We attempted to circumvent these factors by conducting our study in captive, common garden conditions. The ideal experiment though would involve experiments on captive-born animals from both populations because early-life experiences can shape foraging behaviors in adults (Greenberg, 1984; Jones, 1986; Pliner et al., 1993). In addition, it would be interesting to conduct our experiments in the wild to determine if captivity influences feeding behavior and object neophobia. These studies would be especially informative if conducted on sparrows allowed to feed in groups as social foraging is common in this species (Summers-Smith, 1988).

One obvious difference between our sparrow populations that also may have affected foraging behavior is body size. Invading sparrows may have more readily consumed unfamiliar food sources because of smaller body size and hence higher resource demands (metabolic rate) per unit mass. However, two lines of evidence suggest that this is unlikely: feeding rate on seed and heavier molt in the invading population. The first was not different between populations; the second varied, but in the opposite direction of what would be expected. Still, other physiological or morphological differences between populations may yet be important. Physiological responsiveness to stress is known to be distinct between these two sparrow populations (Martin et al., 2005) and may affect neophobia as in other vertebrate species (Cavigelli and McClintock, 2003; Clarke et al., 1988).

In sum, our study does provide some of the first empirical support for a known correlate of invasion success in birds: behavioral plasticity. Although we cannot definitively show that invasion status alone drives dietary preference variation between our populations, by conducting our experiments on captive wild populations of one species, we were able to avoid the problems inherent to interspecific comparisons attempting to identify mechanisms underlying invasive species success (Cassey, 2001; Green, 1997; Sol and Lefebvre, 2000). Moreover, we cannot yet conclude that the differences in foraging behavior we detected between these two populations represent the feeding predispositions of other sparrow populations. Although two-population (species) comparisons must be conservative in their interpretation, our common-garden approach to our study question provides a starting point for more rigorous investigation of additional populations or species. Indeed, further study of other invasive and resident populations is critical to determine if differences in behavioral (Sol and Lefebvre, 2000) and physiological (Lee and Klasing, 2004) flexibility underlie the expansion of species' native ranges (Davis et al., 2001).

We thank Martin Wikelski, Michaela Hau, Silke Berger, Melissa Bowlin, Pierre-Yves Henry, Kelly Lee, Karin Lindström, Nicole Perfito, Thomas Rödl, Dustin Rubenstein, Alex Scheuerlein, and Laura Spinney for discussion. Also, we thank Stephen Fitzgerald, Pierre-Yves Henry, Michelle House, Kelly Lee, Louis Lefebvre, Claudia Mettke-Hofmann, Leah Pyter, Brian Trainor, Zachary Weil, Martin Wikelski, Marlene Zuk, and an anonymous reviewer for comments on previous drafts. Funding was provided by NSF-IRCEB #0212587 to Martin Wikelski and the Environmental Protection Agency STAR Fellowship program to L.B.M. All work was approved by the Princeton University Institutional Animal Care and Use Committee (protocol number 1492), the National Environmental Authority of Panama (ANAM), and the Smithsonian Tropical Research Institute (STRI) and met the animal care standards required by the National Institutes of Health Publication 86-23 and current U.S. laws.

REFERENCES

Beissinger SR, Donnay TJ, Walton R, 1994. Experimental analysis of diet specialization in the snail kite: the role of behavioural conservatism. Oecologia 100:54–65.

Bolivar VJ, Flaherty L, 2004. Genetic control of novel food preference in mice. Mamm Genome 15:193–198.

Cassey P, 2001. Determining variation in the success of New Zealand land birds. Global Ecol Biogeogr 10:161–162.

Cavigelli SA, McClintock MK, 2003. Fear of novelty in infant rats predicts adult corticosterone dynamics and an early death. Proc Natl Acad Sci USA 100:16131–16136.

Clarke AS, Mason WA, Moberg GP, 1988. Differential behavioural and adrenocortical responses to stress among three macaque species. Am J Primatol 14:37–52.

Coleman K, Wilson DS, 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. Anim Behav 56: 927–936.

Coleman SL, Mellgren RL, 1994. Neophobia when feeding alone or in flocks in zebra finches, *Taeniopygia guttata*. Anim Behav 48:903–907.

Cowan PE, 1977. Neophobia and neophilia: new-object and new-place reactions of three *Rattus* species. J Comp Physiol Psychol 91:63–71.

Davis MA, Thompson K, Grime J, 2001. Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. Divers Distrib 7:97–102.

Duncan RP, Blackburn TM, Sol D, 2003. The ecology of bird introductions. Annu Rev Ecol Evol Sys 34:71–98.

Ehrlich P, 1989. Attributes of invaders and the invading process: vertebrates. In: Biological invasions: a global perspective. (Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FG, eds). Chichester: Wiley; 315–328.

Galef B, 1993. Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission. Anim Behav 46:257–265.

Green RE, 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. J Anim Ecol 66:25–35.

Greenberg R, 1983. The role of neophobia in foraging specialization in some migrant warblers. Am Nat 123:444–453.

Greenberg R, 1984. Neophobia in the foraging-site selection of a neotropical migrant bird: an experimental study. Proc Natl Acad Sci USA 81:3778–3780.

Greenberg R, 1990a. Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. Anim Behav 39: 375–379.

Greenberg R, 1990b. Ecological plasticity, neophobia, and resource use in birds. Stud Avian Biol 13:431–437.

Greenberg R, Mettke-Hofmann C, 2001. Ecological aspects of neophobia and neophilia in birds. Curr Ornithol 16:119–178.

Gwinner E, Schwabl H, Schwabl-Benzinger I, 1988. Effects of food deprivation on migratory restlessness and diurnal activity in the Garden Warbler *Sylvia borin*. Oecologia 77:321–326.

Haemig PD, 1989. A comparative experimental study of exploratory behaviour in Santa Cruz Island and Mainland California Scrub Jays *Aphelocoma coerulescens*. Bird Behav 8:38–42.

Heinrich B, Marzluff J, Adams W, 1995. Fear and food recognition in naïve common ravens. Auk 112:499–503.

Immelmann K, Beer C, 1989. A dictionary of ethology. Cambridge: Harvard University Press.

Johnston R, Selander R, 1964. House sparrows: rapid evolution of races in North America. Science 144:548–550.

Jones RB, 1986. Responses of domestic chicks to novel food as a function of sex, strain and previous experience. Behav Proc 12: 261–271.

Kendeigh SC, 1976. Latitudinal trends in the metabolic adjustments of the house sparrow. Ecology 57:509–519.

Lee KA, Klasing KC, 2004. A role for immunology in invasion biology. TREE 19:523–529.

Lee KA, Martin LB, Wikelski M, in press. Responding to inflammatory challenges is less costly for a successful avian invader, the house sparrow (*Passer domesticus*), than its less invasive congener. Oecologia (in press).

Legendre S, Clobert J, Møller A, Sorci G, 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerine introduced to New Zealand. Am Nat 153:449–463.

Lever C, 1987. Naturalized birds of the world. New York: Longman Science Tech.

Lodge DM, 1993. Biological invasions: lessons for ecology. TREE 8: 133–136.

Long J, 1981. Introduced birds of the world. Sydney, Reed.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA, 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710.

Marchetti K, Price T, 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biol Rev Camb Philos Soc 64:51–70.

Martin LB, Gilliam J, Han P, Lee K, Wikelski M, 2005 Corticosterone suppresses immune function in temperate but not tropical House Sparrows. Gen Comp Endocrinol 140:126–135.

Martin LB, Pless M, Svoboda J, Wikelski M, 2004. Immune activity in temperate and tropical house sparrows: a common garden experiment. Ecology 85:2323–2331.

Mayr E, 1965. The nature of colonizing bird species. In: The genetics of colonizing species (Baker HG, Stebbins GL, eds). New York: Academic Press; 29–43.

McClain DK, Moulton MP, Sanderson JG, 1999. Sexual selection and extinction the fate of plumage dimorphic and plumage-monomorphic birds introduced to islands. Evol Ecol Res 1: 549–565.

Mettke-Hofmann C, Winkler H, Leisler B, 2002. The significance of ecological factors for exploration and neophobia in parrots. Ethology 108:249–272.

Minvielle F, Mills AD, Faure JM, Monvoisin JL, Gourichon D, 2002. Fearfulness and performance related traits in selected lines of Japanese quail (*Coturnix japonica*) Poult Sci 81:321–326.

Mitchell D, 1976. Experiments on neophobia in wild and laboratory rats: a re-evaluation. J Comp Physiol Psychol 90:190–197.

Murphy L, 1978. The practical problems of recognizing and measuring fear and exploitation behaviour in the domestic fowl. Anim Behav 26:422–431.

Newsome AE, Noble IR, 1986. Ecological and physiological characters of invading species. In: Biological invasions (Groves RH Burdon JJ, eds). Cambridge: Cambridge University Press; 1–20.

Pliner P, Pelchat M, Grabski M, 1993. Reduction of neophobia in humans by exposure to novel foods. Appetite 20:111–123.

Pulliam HR, 1986. Niche expansion and contraction in a variable environment. Am Zool 26:71–79.

Ridgely R, Gwynne J Jr, 1989. A guide to the birds of Panama with Costa Rica, Nicaragua, and Honduras, 2nd ed. Princeton: Princeton University Press.

Sakai A, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen RE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG, 2001. The population biology of invasive species. Annu Rev Ecol Syst 32: 305–332.

Sol D, Lefebvre L, 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90:599–605.

Sol D, Timmermans S., Lefebvre L, 2002. Behavioural flexibility and invasion success in birds. Anim Behav 63:495–502.

Sorci G, Møller AP, Clobert J, 1998. Plumage dichromatism of birds predicts introduction success in New Zealand. J Anim Ecol 67: 263–269.

Summers-Smith JD, 1988. The sparrows: a study of the genus *Passer*. Carlton: T & AD Poyser.

Thebaud C, Simberloff D, 2001. Are plants really larger in their introduced ranges? Am Nat 157:231–236.

Veltman CJ, Nee S, Crawley MJ, 1996. Correlates of introduction success in exotic New Zealand birds. Am Nat 147:542–557.

Viet RR, Lewis MA, 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. Am Nat 148:255–274.

Visalberghi E, Addessi E, 2000. Seeing group members eating a familiar food enhances the acceptance of novel food in capuchin monkeys. Anim Behav 60:69–76.

Webster S, Lefebvre L, 2001. Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. Anim Behav 62:23–32.

Weins JA, Dyer MI, 1977. Assessing the potential impact of granivorous birds in ecosystems. In: Granivorous birds in ecosystems (Pinowski J, Kendeigh C, eds). Cambridge: Cambridge University Press; 205–264.

Williamson M, 1996. Biological invasions. London: Chapman and Hall.

Yamamoto ME, de Araújo Lopes F, 2004. Effect of removal from the family group on feeding behaviour by captive *Callithrix jacchus*. Int J Prim 25:489–500.