

Ecomorphology and disease: cryptic effects of parasitism on host habitat use, thermoregulation, and predator avoidance

BRETT A. GOODMAN¹ AND PIETER T. J. JOHNSON²

Ecology and Evolutionary Biology, Ramaley N122, University of Colorado, Boulder, Colorado 80309 USA

Abstract. Parasites can cause dramatic changes in the phenotypes of their hosts, sometimes leading to a higher probability of predation and parasite transmission. Because an organism's morphology directly affects its locomotion, even subtle changes in key morphological traits may affect survival and behavior. However, despite the ubiquity of parasites in natural communities, few studies have incorporated parasites into ecomorphological research. Here, we evaluated the effects of parasite-induced changes in host phenotype on the habitat use, thermal biology, and simulated predator-escape ability of Pacific chorus frogs (*Pseudacris regilla*) in natural environments. Frogs with parasite-induced limb malformations were more likely to use ground microhabitats relative to vertical refugia and selected less-angled perches closer to the ground in comparison with normal frogs. Although both groups had similar levels of infection, malformed frogs used warmer microhabitats, which resulted in higher body temperatures. Likely as a result of their morphological abnormalities, malformed frogs allowed a simulated predator to approach closer before escaping and escaped shorter distances relative to normal frogs. These data indicate that parasite-induced morphological changes can significantly alter host behavior and habitat use, highlighting the importance of incorporating the ubiquitous, albeit cryptic, role of parasites into ecomorphological research.

Key words: *habitat use; malformation; parasite manipulation; performance; physiology; thermal biology.*

INTRODUCTION

Natural selection shapes the traits of organisms to effectively use the habitats they occupy (Karr and James 1975, Miles and Ricklefs 1984). Because morphology is directly linked to locomotion (Arnold 1983, Brodie 1992), even subtle changes in morphology can have major effects on an organism's ability to use its environment effectively. While numerous studies have illustrated how organisms adapt morphologically to their environment (Irschick and Losos 1999, Goodman et al. 2008), few have considered the role of a cryptic yet ubiquitous influence on how organisms use their environment: parasite infection and disease.

Despite their diversity and abundance, parasites and pathogens are frequently overlooked in ecological research (Lafferty et al. 2008). Some parasites cause changes in host phenotype (e.g., behavior, morphology, and/or physiology), ranging from subtle shifts in behavior to the creation of new niches and habitats (Mouritsen and Poulin 2005). Because many parasites

depend on predation as a mechanism of transmission (trophic transmission), such alterations are hypothesized to enhance the passage of parasites from one host to another (Poulin 1994, Moore 2002). As a result, parasite infection can create cryptic phenotypic subgroups within a species, which differ in ecological traits and even reproductive compatibility (Vala et al. 2004). Detecting these subgroups can be difficult without intensive study or necropsy, however.

Infection by the trematode *Ribeiroia ondatrae* induces a particularly severe form of morphological change in its amphibian hosts, including both missing and extra limbs (Johnson et al. 2002). This extreme form of phenotypic manipulation is hypothesized to increase parasite transmission by increasing predation ("parasite-induced trophic transmission"; Lafferty 1999, Johnson et al. 2004). Empirical and theoretical research on ecomorphology has repeatedly emphasized the survival value of effective locomotor performance (Jayne and Bennett 1990, Langerhans and DeWitt 2004), suggesting that parasite-induced malformations have the potential to alter host interactions with the environment and, consequently, survival. Previous work (e.g., Relyea 2002, Relyea and Auld 2002) has demonstrated the importance of predator- and competitor-induced morphological changes in amphibians, but few studies have similarly examined the phenotypic effects of parasites.

Manuscript received 10 March 2010; revised 14 September 2010; accepted 30 September 2010. Corresponding Editor: M. C. Urban.

¹ Present address: Ecology and Evolutionary Biology, School of Earth and Environmental Sciences, University of Adelaide, SA 5005 Australia.

² Corresponding author.
E-mail: pieter.johnson@colorado.edu

For amphibians, the transition from aquatic to terrestrial environments places strong selection on the development of a terrestrial locomotor system. Alongside the effects of malformations on predator escape, changes in morphology may also affect host behavior, locomotor performance, and habitat use. However, whether changes in host performance are caused directly by morphological deformities or indirectly owing to other parasite-induced changes (e.g., behavior, physiology) remains unexplored. Because the parasite *Ribeiroia ondatrae* only causes malformations when tadpoles are infected during susceptible stages of development (Schotthoefer et al. 2003), individuals co-occurring within the same pond are typically infected with the parasite but exhibit considerable variation in malformations. Infected individuals range from having externally normal features to being completely immobilized in both hind limbs (Johnson et al. 2002), thus providing a rare opportunity to disentangle the direct effects of infection from those involving changes in body plan.

To broadly evaluate the effects of parasite-induced morphological changes on the ecomorphological relationships of amphibian hosts, we examined the microhabitat use of normal and malformed frogs from ponds supporting *R. ondatrae*. We evaluated how malformation status affected (1) microhabitat use, including use of available habitats in and around a pond, (2) thermal ecology, including differences in substrate and body temperatures, and (3) predator-avoidance responses such as threat tolerance and escape distance. This approach enabled us to define whether changes in ecomorphology and habitat use were the result of parasite-induced changes in morphology vs. parasite-induced physiological effects. Because of the ecomorphological importance of hind limbs in amphibian locomotion, we predicted that malformations would impair affected frogs' ability to occupy optimal habitats (Zug 1978, Losos 1990), exposing them to higher temperatures and greater predatory threat.

METHODS

Natural history and study system.—The trematode parasite *Ribeiroia ondatrae* has a complex life cycle involving transmission among bird or mammal definitive hosts, snail intermediate hosts, and amphibian or fish second intermediate hosts (Johnson et al. 2004). The parasite reproduces asexually within planorbid snails, releasing free-swimming cercariae into the aquatic environment that encyst around the developing limbs of larval amphibians, including those of the species examined in this study the Pacific chorus frog (*Pseudacris regilla*), and frequently cause developmental malformations, including extra, missing, or malformed limbs (Johnson et al. 2002). Because of the difficulty in reliably detecting subtle, internal malformations, we only considered frogs with obvious malformations such as deformed limbs and digits. To test whether infection intensity was related to the presence of malformations,

we quantified *R. ondatrae* metacercariae from a subsample of normal and malformed frogs from two ponds in East Bay, California, with high levels of infection and malformations (Quick Pond, Contra Costa County, area = 2234 m², $n = 133$ frogs; Rosendin Pond, Santa Clara County, area = 7309 m², $n = 27$ frogs; see Plate 1).

Measurement of frog microhabitat use.—We assessed the structural microhabitat use of externally normal and malformed frogs by walking 54 haphazard linear transects, each of which was 8–10 m in length and perpendicular to the shoreline. To prevent disturbing active frogs, we commenced transects from within the pond and scanned the shoreline for undisturbed individuals. We collected data on randomly selected frogs (i.e., one malformed and one non-malformed) within 3 minutes of one another and alternated data collection between malformed and non-malformed frogs (when malformations could be reliably assessed from >1 m distance). For each frog observed, we recorded its microhabitat usage, its vertical height above substrate (using a 2 m long flexible measuring tape), its body angle and perch angle (degrees, using a protractor). We also recorded body temperature (T_b) and microhabitat (substrate) temperature (T_s) using a hand-held infrared thermometer (Fluke 62 Mini; Fluke, Everett, Washington, USA), and sun exposure (full sun, partial sun, and shade). We defined three microhabitat categories that commonly occurred around ponds: (1) bare earth/leaf litter/debris (exposed earth and low piles of leaf litter, sticks, or flattened grass or other vegetation < 0.2 m high); (2) *Juncus*/grass (patches of either *Juncus* and/or grass 0.2–0.6 m high); and (3) bulrush/cattail (patches of bulrush and/or cattail > 0.6 m high). Both ponds contained similar proportions of each microhabitat type (Quick, 18% bare earth/leaf litter/debris, 68% *Juncus*/grass, and 14% cattail; Rosendin, 22% bare earth/leaf litter/debris, 69% *Juncus*/grass, and 9% bulrush/cattail). Finally, we assessed each frog's malformation type (if present) at the end of each transect.

Predator response behavior.—We examined the response behavior of normal and malformed frogs to a simulated predator (i.e., an approaching human) by measuring approach- and escape distance. Prior to each trial, we scanned the shoreline for an individual frog to approach directly at a constant speed (4 km/h). We commenced each "predator" approach trial by wading toward shore from >4 m offshore. Equivalent numbers ($N = 54$) of non-malformed and malformed frogs were approached and we alternated between normal and malformed frogs. We conducted trials only on clear days, wearing clothes of identical colors, and performed only a single trial in the given area of pond habitat on a given day. At the moment a frog moved from its initial undisturbed perch position, the position of the observer was recorded (distance from frog). Each frog was observed until it stopped escaping and sought refuge, at which point the "escape distance" from the initial position was recorded along with refuge height.

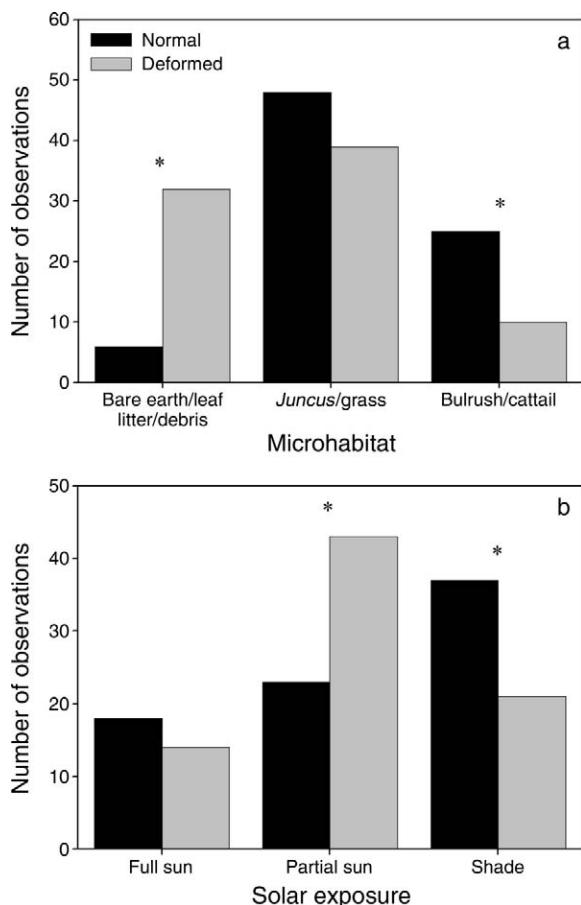


FIG. 1. (a) The microhabitat use and (b) the solar exposure of malformed and non-malformed frogs at ponds in the East Bay region of California. Microhabitat use and solar exposure were assessed by alternating observations on malformed and non-malformed frogs ($N = 160$ observations). Asterisks indicate significant differences ($P < 0.05$) between malformed and non-malformed frogs for microhabitat use and solar exposure categories.

Analyses.—To test for differences in microhabitat use, substrate and body temperature, and predator response behavior, we used ANOVA and Kruskal-Wallis non-parametric ANOVA. Because comparisons of microhabitat use by malformed and non-malformed frogs revealed no significant differences between ponds (microhabitat type, all $P > 0.103$; thermal microsites, all $P > 0.200$; solar exposure, all $P > 0.678$; and perch height and angle, all $P > 0.082$), we pooled all data prior to analyses of microhabitat use. We compared the use of different microhabitats and solar exposure by malformed and non-malformed frogs using a goodness-of-fit test (Zar 1996). We used all-means (Tukey hsd) comparisons for post hoc tests. Because tests of collinearity revealed a strong correlation between perch angle and body angle ($r = 0.85$, $N = 160$ observations), we included only perch angle in the model of microhabitat use. Finally, to test which microhabitat had the

greatest effect on body temperature, we selected among the candidate models using backwards, stepwise regression and AIC (Akaike's information criterion).

RESULTS

We found no significant differences in the intensity of *Ribeiroia* infection between normal and malformed frogs from either pond (Quick, mean infection in normal and malformed frogs = 18.9 and 26.1, respectively, $t = -1.613$, $P = 0.110$; Rosendin, mean infection in normal and malformed frogs = 36.2 and 42.4, respectively; $t = -0.749$, $P = 0.461$); however, malformation status was associated with differences in nearly all of our other measured response variables. Malformed ($N = 80$) and normal ($N = 80$) frogs differed significantly in microhabitat use ($\chi^2 = 25.13$, $P < 0.001$; Fig. 1a). Malformed frogs used bare earth/leaf litter/debris substrates more frequently than non-malformed frogs ($\chi^2 = 19.53$, $P < 0.001$), whereas externally normal frogs used bulrush/cattails more than malformed frogs did ($\chi^2 = 6.64$, $P = 0.01$; Fig. 1a). We found no differences in the use of the *Juncus*/grass substrates ($\chi^2 = 0.933$, $P = 0.334$). Non-malformed and malformed frogs also differed in the amount of solar exposure in perching areas ($\chi^2 = 10.97$, $P < 0.05$; Fig. 1b), with malformed frogs using partial sun more frequently than non-malformed frogs ($\chi^2 = 6.06$, $P < 0.05$; Fig. 1b). Normal frogs also selected shaded sites more frequently than did malformed frogs ($\chi^2 = 4.41$, $P < 0.05$; Fig. 1b). However, there was no significant difference in the proportion of non-malformed and malformed frogs that selected microhabitats in full sun ($\chi^2 = 0.50$, $P = 0.479$; Fig. 1b).

Relative to normal frogs, malformed individuals selected perches closer to the substrate (ANOVA, $F_{1,154} = 47.89$, $P < 0.001$; Fig. 2a), used perches with less extreme angles (ANOVA, $F_{1,54} = 26.24$, $P < 0.001$; Fig. 2b), and perched with their body on a weaker angle (ANOVA, $F_{1,54} = 27.36$, $P < 0.001$; Fig. 2c). Malformed frogs ($N = 26$) also exhibited a higher threat tolerance, allowing a simulated predator to approach significantly closer than did non-malformed ($N = 28$) frogs (ANOVA, $F_{1,52} = 10.07$, $P < 0.0001$; Fig. 2d). Once an escape response had been initiated, malformed frogs moved a shorter distance away from the potential predator (ANOVA, $F_{1,52} = 14.56$, $P < 0.0001$; Fig. 2e) and used refugia nearer to the ground in comparison with non-malformed frogs (ANOVA, $F_{1,52} = 4.41$, $P < 0.05$; Fig. 2f). The specific types of refugia used by malformed and normal frogs did not differ ($\chi^2 = 2.443$, $P = 0.118$).

Microhabitats occupied by malformed frogs ($N = 71$) were significantly warmer than those used by non-malformed frogs ($N = 62$; ANOVA, $F_{1,131} = 10.07$, $P = 0.0019$; Fig. 2g). On average, bare earth/leaf litter/debris substrates, which were often used by malformed frogs, were significantly warmer than the bulrush/cattail microhabitats often used by normal frogs (hsd, $P < 0.05$); *Juncus*/grass and bare earth/leaf litter/debris

substrates did not differ in temperature ($P > 0.05$). Correspondingly, malformed frogs had higher external body temperatures than their non-malformed counterparts (ANOVA, $F_{1,131} = 17.58$, $P < 0.0001$; Fig. 2h). A backward, stepwise, multiple-regression model with frog body temperature as the dependent variable and deformity status, substrate category, perch height, perch angle, and solar exposure as independent variables, identified a negative effect for perch angle ($F = 5.053$, $P < 0.05$), a positive effect of bare earth/leaf litter/debris substrates ($F = 10.651$, $P = 0.001$) and a positive effect for malformation status ($F = 10.245$, $P = 0.002$; adjusted $R^2 = 0.16$, $df = 4$, $N = 128$, $F_{1,133} = 8.856$, $P < 0.001$).

DISCUSSION

Despite the sometimes-dramatic changes caused by parasitism (Moore 2002), parasite-induced changes in host morphology have historically been omitted from ecomorphological research. In the current study, phenotypic changes caused by trematode infection significantly affected how amphibian hosts interacted with and utilized their surrounding environment. Relative to normal frogs, malformed individuals used ground microhabitats more frequently than vertical substrates, perched on less angled perches closer to the ground, and occurred in hotter microhabitats. Malformed frogs also had higher body temperatures than non-malformed frogs, which likely resulted from differences in microhabitat use and the corresponding amount of sun exposure. Perhaps most importantly, morphologically altered frogs allowed a simulated predator to approach closer before initiating an escape response, escaped over shorter distances once a response was initiated, and remained closer to the ground than non-malformed frogs after escaping. Given that malformed and non-malformed frogs exhibited comparable levels of *Ribeiroia* infection, the observed differences in habitat use, thermal biology, and predator responses between these two groups most likely resulted directly and indirectly from the malformations, rather than from unquantified physiological changes associated with infection.

How do parasite-induced malformations cause differences in the habitat use of malformed frogs? For recently metamorphosed *P. regilla*, the pond environment presents many structures and media through which locomotion must occur. Frogs are required to swim through water, climb up and over vertical structures, and jump to and among preferred refugia (Duellman and Trueb 1994). Recently metamorphosed frogs must perform these activities while attempting to capture prey and avoid predation. The frog body plan is well suited to cope with such ecological challenges, and the relationship between frog morphology and performance is well established (Zug 1978). Any reduction in the ability to jump accurately, such as malformations of the hind limbs for example, likely translates into a decreased ability to use higher perches and vertical habitat

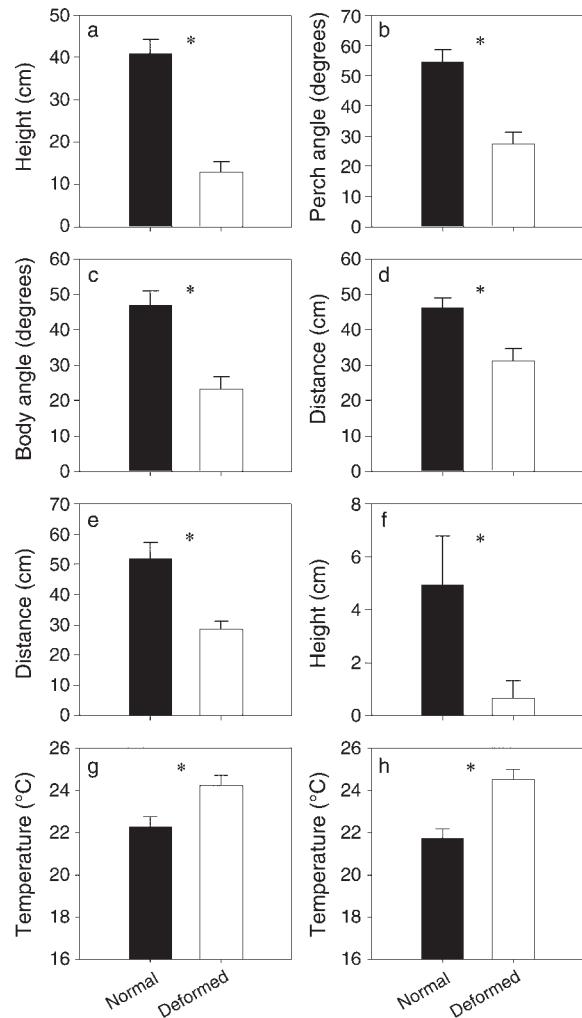


FIG. 2. (a–c) Perch use, (d–f) behavioral responses to a potential predator, and (g–h) thermal microsite selection by malformed (white bars) and non-malformed (black bars) frogs at ponds in the East Bay region of California. Presented are (a) perch height (cm above the ground), (b) perch angle, (c) body angle, (d) distance before commencing escape, (e) distance escaped, (f) height of refuge selected after commencing escape from a potential predator, (g) substrate temperature (T_s), and (h) frog body surface temperature (T_b) for malformed and non-malformed frogs ($N = 160$ observations). Values shown are means \pm SE. Asterisks indicate significant differences ($P < 0.05$) between malformed and non-malformed frogs.

structures, such as bulrush/cattail habitats in the current study. Because of effects on a frog's ability to apply equal propulsive forces when jumping, limb malformations likely reduce jumping accuracy for landing on smaller perches (Zug 1978), which helps explain why malformed frogs were found primarily on low angle perches, typically on bare earth. Experimental studies focused on the performance of normal and malformed frogs have demonstrated the deleterious effects of limb deformities on the jumping, swimming, and prey capture

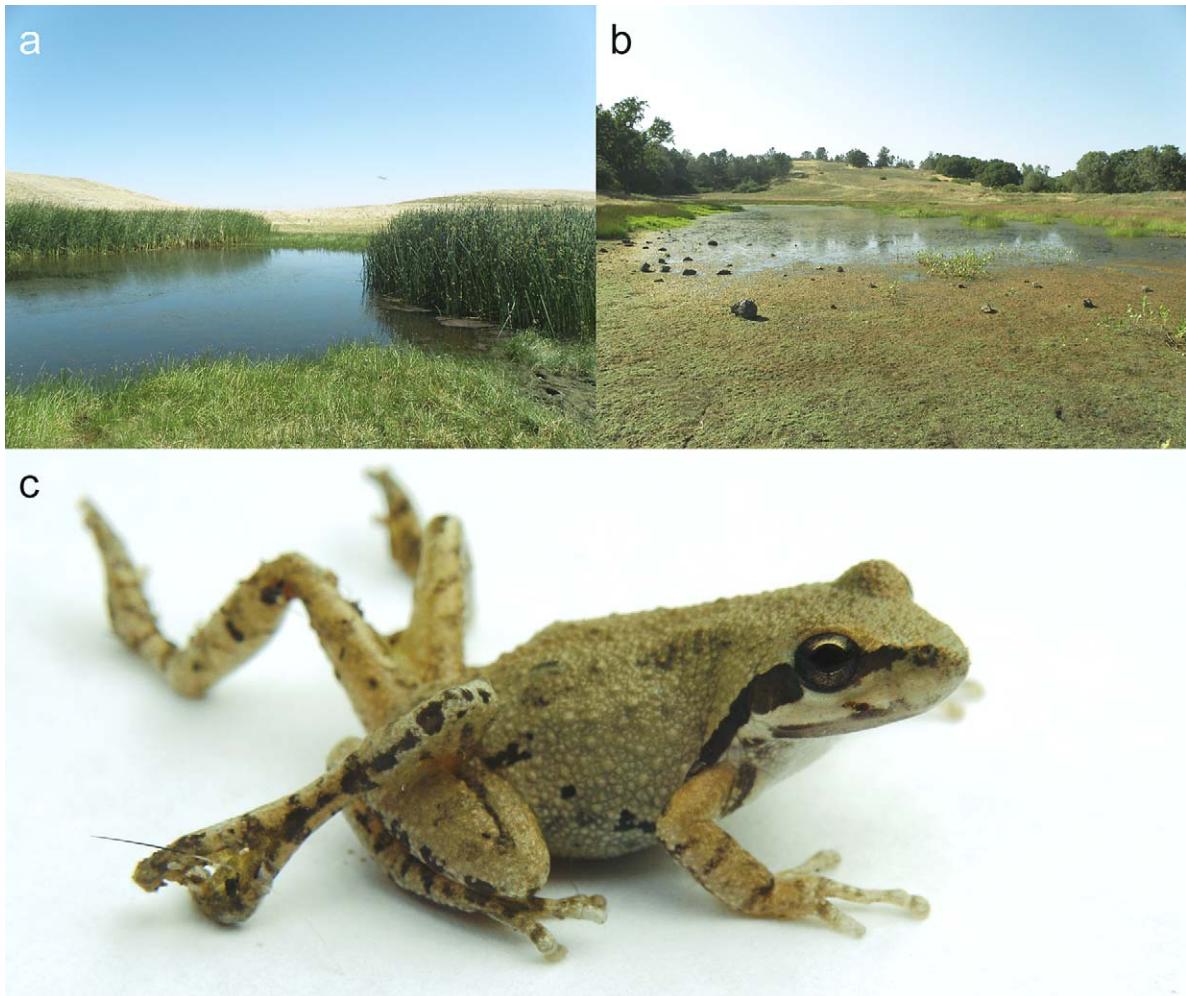


PLATE 1. Field sites and organisms used to study ecomorphology and disease. (a) Quick Pond and (b) Rosendin Pond, which illustrate the habitat types in which normal and malformed frogs were studied (i.e., bare earth, short grass (*Juncus*), and taller macrophytes (bulrush/cattails)). (c) A Pacific chorus frog (*Pseudacris regilla*) with representative limb malformations caused by trematode parasite infection. Photo credits: B. A. Goodman.

abilities of *P. regilla* (B. Goodman and T. Johnson, *unpublished manuscript*).

The observed differences between malformed and normal frogs may have important implications for amphibian survival and parasite transmission. Relative to normal frogs, malformed animals used bare earth/leaf litter/debris substrates more frequently, bulrush/cattail substrates less frequently, and perched closer to the ground. For the majority of ponds in the East Bay region of California, USA, bulrush/cattail macrophytes (*Scirpus* and *Typha* spp.) are the tallest vertical structures and offer a safe harbor from both potential predators and daily extremes in temperature (Rorabaugh et al. 2004). Garter snakes (*Thamnophis* spp.), for example, which are a primary predator of many pond-breeding amphibian species, rarely climb elevated microhabitats to obtain prey (Rossman et al. 1996). High perches might also afford protection from

predatory water birds (e.g., herons), which are the definitive hosts of *R. ondatrae*, suggesting that closed, more complex microhabitats represent a safe harbor from terrestrial and aerial predators alike (Snell et al. 1988).

By reducing the ability of malformed frogs to utilize such refugia, parasite-induced malformations may increase predation on such individuals, potentially enhancing parasite transmission when predators are suitable hosts. Although this idea has been suggested previously (Sessions and Ruth 1990, Johnson et al. 2002), our results indicate that the effects of malformations on predation risk are more varied and multifaceted than previously hypothesized, extending beyond direct impairment of locomotion. While both normal and malformed frogs attempted to escape an impending predation threat, malformed frogs allowed the potential predator to approach closer, moved a shorter distance,

and moved into refugia that were closer to the ground than non-malformed frogs, each of which may increase their predation risk. These results are consistent with a growing body of literature highlighting the ability of some parasites to cause changes in host behavior that may increase the probability of predation, thereby aiding transmission to the next stage of the parasite life cycle (Poulin 1994, Moore 2002). A critical assumption of the parasite manipulation hypothesis is that induced changes increase the risk of predation by definitive hosts specifically, rather than by predators that do not function as hosts. Although a thorough test of whether malformations significantly enhances transmission is beyond the scope of this study, we suggest that such effects will be particularly pronounced for the definitive hosts of *R. ondatrae* (i.e., predatory water birds) because of their reliance on movement to detect prey. For other predators that rely more heavily on vision and chemoreception to locate prey (e.g., garter snakes), malformations may have less substantial effects on host susceptibility to predation (Rossman et al. 1996). However, additional research comparing the effects of malformations on actual rather than simulated predation threats are needed to test this hypothesis.

Relative to other examples of parasite manipulation, *Ribeiroia*-induced malformations in frogs stand out in terms of the severity of gross morphological changes induced by infection, which involve changes not just in host appearance or behavior but in the entire body plan. Because both normal and malformed frogs supported comparable levels of infection, observed differences in predator response most likely owe directly or indirectly to the malformations themselves, rather than to infection-induced variation in sensory modalities such as vision and chemoreception. Thus, the differences observed in this study likely reflect either decreased mobility associated with malformations, such that malformed frogs are less effective at escaping predators, or increased lethargy caused by reduced energy intake, whereby malformed frogs are less effective at prey capture and therefore have less energy.

Parasite-induced changes in frog morphology were also associated with higher host body temperatures due to differences in microhabitat use. Malformed individuals were more likely to occur in partial sun (rather than shade) and on bare ground substrates closer to the ground (rather than on vertical refugia). Based on our measurements of substrate temperatures, these differences in microhabitat selection likely resulted in malformed frogs experiencing higher temperatures. At least two plausible hypotheses may explain this finding. First, malformed frogs could select warmer habitats in order to raise their body temperature and induce "behavioral fevers," as noted for other amphibian species in response to parasite infection (Sherman et al. 1991). While cases of dose-dependent behavioral fever (i.e., only chronically infected individuals elevate body temperature) are known for amphibians (Sherman

2008), we argue that this is unlikely to be the case here. Despite the absence of malformations, all individuals (malformed and normal) were infected with comparable levels of *Ribeiroia*, suggesting that differences in infection alone do not explain the observed behavioral differences in thermoregulation. Instead, the inability to climb above or avoid substrates of greater temperature likely explains the elevation in body surface temperature of malformed frogs. Indeed, many lizards climb onto elevated vertical perches in the hottest part of the day to escape the direct incident solar radiation experienced closer to the ground (Heatwole and Taylor 1987). Frogs on elevated perches can also orient their bodies to reduce direct incident solar radiation, further increasing cooling due to greater air movement at vertical heights (Heatwole and Taylor 1987). A potential implication of this result is that malformed frogs are more prone to overheating and desiccation in such habitats, where summer daytime shade temperatures often exceed 37°C.

An impaired ability to occupy thermal refugia and reduce ambient body temperature may also affect thermal performance. In ectotherms, optimal performance ability is restricted to a relatively narrow temperature range; any time spent above the critical thermal threshold can compromise locomotor performance and impair an individual's ability to escape from predators or sudden temperature changes (Reading 2007). While amphibians display fairly wide thermal performance functions (Navas et al. 2008), performance becomes impaired rapidly with increases in temperature (Huey and Stevenson 1979). Thus, the higher body surface temperatures of malformed individuals could predispose them to overheating, desiccation, or operating outside of their preferred thermal range. Ultimately, such effects could increase the probability of mortality in those frogs with parasite-induced alterations, either directly by exceeding thermal limits or indirectly through predation.

Studies of ecomorphology have advanced our understanding of organismal adaptation to the environment (Miles and Ricklefs 1984, Irschick and Losos 1999, Relyea 2002). Despite these advances, little consideration has been afforded to parasites, and how they influence the effective habitat use of infected organisms. We emphasize the value of incorporating parasites into ecomorphological research. Because parasites can affect many dimensions of their hosts (e.g., morphology, behavior, physiology, and reproduction; Poulin 1994), the integration of ecomorphology, habitat use, and disease ecology has enormous potential to provide novel insights for both disciplines. Selection of suitable candidate systems with obvious changes in phenotypes (e.g., some amphibians, gastropods, zooplankton, and fishes) may provide efficient mechanisms to understand the ecological and evolutionary significance of key functional traits and the likely impacts of climate change on animal groups.

ACKNOWLEDGMENTS

The authors thank K. Dosch, D. Preston, and M. Baragona for field assistance, and I. Buller, S. Orlofske, and D. Larson for help with amphibian necropsies. For property access, we thank East Bay Regional Parks, Santa Clara County Parks, and especially D. Rocha, S. Bobzien, and S. Quick. B. A. Goodman thanks J. Isaac for advice on project design and feasibility. The work was part of a grant from the NSF (DEB-0841758) and the David and Lucile Packard Foundation to P. T. J. Johnson.

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