

Jos. J. Schall · Christine M. Staats

Parasites and the evolution of extravagant male characters: *Anolis* lizards on Caribbean islands as a test of the Hamilton-Zuk hypothesis

Received: 10 January 1997 / Accepted: 24 March 1997

Abstract *Anolis* lizards from Puerto Rico (five species from one site), Curaçao and Aruba in the southern Caribbean (2 populations), and 22 populations from 14 islands in the eastern Caribbean were surveyed for blood parasites (two species of *Plasmodium* and haemogregarines). Literature records for gut helminths from nine of these populations were added to the data set. Dorsal body color and dewlap color of males were also observed and classified into objective classes with no subjective view of showiness. These data were used to test the among-species prediction of the Hamilton-Zuk hypothesis which states that species harboring more harmful parasites over their evolutionary history will be more likely to evolve extravagant sexually dimorphic traits. Critics have noted important shortcomings in previous tests of the prediction; here we corrected for these errors. Parasite loads (prevalence and number of species) and dorsal and dewlap color varied substantially among the populations sampled. However, there was no association of parasite load with color either in a broad analysis or when correcting for phylogenetic relationships among the lizard species.

Key words Sexual selection · Hamilton-Zuk hypothesis · *Anolis* · Malaria

Introduction

Males of many animal species possess flamboyant morphological features that are lacking in the relatively drab females. Darwin's hypothesis of sexual selection proposes that such ornaments, although costly to produce and maintain, are advantageous because they act as "charming" signals to females during mate selection.

Any reduction in the survival component of fitness caused by the ornament would be more than offset by an increase in mating success enjoyed by the extravagant male (review in Andersson 1994).

Although female choice may be a potent force favoring the evolution of ornaments by males, how do females benefit from their selection of extravagant males? Once female choice becomes established in the population, any female not selecting a showy male may produce sons that would have difficulty finding a mate in the next generation. The original benefit for females in choosing the showy mate may no longer exist, yet female preference for the trait continues. However, females may also incur costs in seeking and selecting only males with the showy trait (Pomiankowski 1987), and this might weaken the selective pressure toward female choice and the maintenance of the showy trait by males.

Two hypotheses offer an explanation for the origin and maintenance of extravagant traits in males. The first proposes that random biases in the sensory system of some species leads females to favor males with some useless feature (Ryan and Keddy-Hector 1992). Thus, females gain no benefit initially from their preference, and eventually benefit only because they produce "sexy sons." The second hypothesis argues that the extravagant trait contains information about the genetic quality of the male; females can capture "good genes" for their offspring by mating with the most showy male.

The good genes hypothesis is intuitively pleasing, but requires demonstration of the exact kind of information being passed to females by the appearance of the male's ornament. Hamilton and Zuk (1982) proposed that the appearance of a showy trait contains information about the male's parasite load. Males infected with parasites would appear scrofulous in general, and the ornament's appearance would suffer most severely. Females could then pick mates that carry low parasite burdens, and are thus likely to possess a genotype that confers resistance to specific parasites. Parasites are extremely abundant and diverse biologically, so resistance to one kind of parasite would not guarantee resistance to others. The

J.J. Schall (✉) · C.M. Staats
Department of Biology,
University of Vermont, Burlington, VT05405, USA
Fax: (802) 656-2914; e-mail: jschall@zoo.uvm.edu

appearance of the showy trait would therefore always contain honest information about the male's genetic quality because different strains or species of parasite would cycle through the host population.

The Hamilton-Zuk hypothesis leads to two testable predictions. For those species with males possessing an extravagant feature, parasitized males will be less showy than infected males. Within populations, the uninfected males should be the most extravagant. Among species, however, those harboring more parasites will be more likely to have evolved conspicuous ornaments in the males. Those species with the most showy males today should be those that have been exploited by the most parasites over their evolutionary history.

Several tests of the among-species prediction have been reported, but these have provoked a blistering controversy among evolutionary biologists and parasitologists (reviewed by Møller 1990; Read 1990; Clayton 1991). The original study of Hamilton and Zuk (1982) established the methods that are typical in among-species tests of the hypothesis. They compared variation in showiness among bird species with the number of parasites infecting each bird species. Experienced bird watchers gave a subjective score to the appearance of North American birds, and, independently, literature data were used to determine the number of species and prevalence of parasites infecting each bird. The analysis found a significant association: bird species that suffer attack by more parasites were those that were more brightly colored.

Critics have noted five major benchmarks required for an ideal among-species test of the Hamilton-Zuk hypothesis. These are:

1. The evolutionary relationships among the species of host must be included in the analysis. A particular evolutionary lineage might be both showy and carry many parasites for independent historical reasons, so each species of host cannot be added into the analysis as though they are independent data (Read and Harvey 1989).
2. The rating of showiness is subjective and results could differ depending on the method used in scoring (Read and Harvey 1989). Human observers can only guess at the sensory response of another species to colors or shapes. Therefore, data on the supposed ornament must be gathered and analyzed in an objective way, without any subjective rating of showiness.
3. Viewing pictures in a book, or watching the animals in nature at one or a few sites, does not respect the variation in the appearance of a wide spread species.
4. Literature records of parasite loads do not tell how widespread the parasites are, or the length of the association of the parasites and hosts. For example, prevalence of parasites of birds varies greatly among geographical regions, time of year, and among years; other kinds of parasite-host systems may vary in parasite loads in similar ways, thus confounding any measure of the long-term association of hosts with

their parasites (Weatherhead and Bennett 1991, 1992; Weatherhead et al. 1991; Merila et al. 1995). The hypothesis proposes that parasites have affected the evolutionary history of their hosts, so information about the duration of the parasite-host association is critical for any test of the hypothesis. To correct for points 3 and 4, the host population must be sampled for appearance of the ornament and for parasite load over its entire geographic range, and evidence of a long-term, fairly stable relationship between the parasites and hosts must be established.

5. The hypothesis assumes parasites harm their hosts, thus providing an opportunity for selection to function, and that parasite infection alters the appearance of the extravagant male trait. Thus, surveys should not examine randomly selected parasites, but only those known to cause harm to the host and alter the trait under study (Zuk 1991).

Meeting these benchmarks makes testing the among-species prediction an onerous task; indeed, Cox (1989) opined that the hypothesis may not be testable at all. Here we present an among-species test of the Hamilton-Zuk hypothesis by comparing the colors of *Anolis* lizards in the Caribbean islands with their parasite burdens. Our study was designed to answer the shortcomings found by critics of previous publications.

Study system and methods

The lizard genus *Anolis* contains approximately 150 species distributed in the Caribbean islands, with many more species on the mainland of North, Central, and South America (Roughgarden 1995). The small islands of the eastern Caribbean support one or two anole species each; endemic species are common, sometimes inhabiting a few islands that were connected in the Pleistocene, and sometimes inhabiting only a single island. Roughgarden (1995) presents evidence that the distribution of anoles in the eastern Caribbean is a result of a combination of tectonic events and ancient overwater transport. Thus, the present distribution of anoles has existed for millions of lizard generations.

We examined 29 *Anolis* populations on 14 islands in the eastern Caribbean, two islands in the southern Caribbean, and at one site in eastern Puerto Rico (Table 1). *Anolis* on these islands vary enormously in body color; males range from a drab tan or brown in some species, to bright green in others, to complex mixtures of color. *A. bimaculatus* on St. Kitts, for example, is a combination of green, blue, yellow, white, and black. Likewise, male anoles possess an enlarged flap of skin under the chin (the dewlap) that can be erected during display. Dewlap color varies among species, from uniform tan and pale yellow, to complex mixtures of yellow, orange, and black. Color paintings of the anoles of the eastern Caribbean in Lazell (1972) illustrate the variation in color among *Anolis* species. For the populations on the Lesser Antilles, we can observe the showy features (body and dewlap color) of each anole population throughout its long-established range, a single island. On a few of the larger eastern islands, such as Dominica, the endemic anole has evolved into distinct subspecies, so colors of these ancient populations can be examined as well.

We made color photographs of the dorsal surface and dewlap of male lizards from each island; on Dominica there is substantial color variation among localities, so these were all sampled as well. Similar color variation exists on Martinique, but we sampled only one of the color morphs. Both dorsal and dewlap colors vary

among individuals in a local population, and dorsal color also can change in an individual anole over time. Therefore, we chose to photograph several males that to us appeared to differ the most from females in that population. We then showed two to five of these photographs as well as the paintings in Lazell (1972) to 14 individuals (with no communication among the members of the panel) who placed each lizard into one of four dorsal color classes and four dewlap color classes. We did not ask the panel members to rank the showiness of the lizards (this would contain a subjective, strictly human bias). The dorsal color classes were: (1) uniform brown or a pattern of tan or brown, including spots or blotch; (2) uniform green, yellow, or some other color other than brown; (3) two colors such as brown and yellow, yellow and green, green and black; (4) more than two colors such as black, green, and yellow. The dewlap classes were: (1) all cream or tan; (2) any other single color; (3) two colors; (4) more than two colors. For all of the lizard populations, 10–14 of the 14 human observers agreed on placement into a color class for both dorsal and dewlap appearance. *Anolis* can see into the ultraviolet, and the degree of reflection of ultraviolet light from dewlaps varies among species (Fleishman et al. 1993). However, the broad color classes used here are likely to be viewed by *Anolis* and human eyes in similar ways.

We surveyed each lizard population for blood parasites. For each island, 2–50 sites were surveyed, depending on island size and the presence of subspecies on the island. A blood smear was made for each lizard and the animal returned to its point of capture. Smears were stained and examined using the methods described in Schall and Bromwich (1994). Two species of *Plasmodium* are common in the Caribbean islands, *P. azurophilum* and *P. floridense*. The distribution of these two species is described in Staats and Schall (1996) and Schall (1996). A biogeographical analysis (Staats and Schall 1996) concluded that malaria was most likely introduced onto each island when the local anole first became established there. That is, the parasites have long coevolved with the *Anolis* of each island. Previous studies in the Caribbean have shown that malaria prevalence does not vary substantially by season or over a few year period (Schall and Vogt 1993; Schall 1996), suggesting our samples give an adequate reflection of the prevalence of *Plasmodium* on the islands. We also scored for presence of haemogregarines, another taxon of blood parasite, but could not identify these parasites to species without knowledge of the invertebrate host. Prevalence and number of species of helminth parasites in the intestines has been reported for nine of our anole populations (Dobson et al. 1992) and is included in the analysis. No information is available on the duration or stability of these helminth parasite-host systems on the islands.

Plasmodium infection causes multiple pathologies for lizard hosts, including *Anolis* (review in Schall 1996). Malarial parasites can also change the sexually dimorphic color of male lizards, perhaps by altering hormonal levels (Ressel and Schall 1989; Dunlap and Schall 1995). The influence of gut-dwelling helminths or haemogregarines on the health of lizards is unknown.

Although the phylogenetic relationships of *Anolis* and related genera are controversial, the species groups used in this study for the eastern Caribbean appear to be reflect the consensus view. Thus, we use the summary cladogram and other information given by Roughgarden (1995) in our phylogenetic analysis.

Results

Table 1 presents the results for the 7092 lizards we sampled, plus 880 lizards sampled for their intestinal parasites by Dobson et al. (1992). Sample sizes vary among the populations we surveyed and could bias the determinations of number of *Plasmodium* species and their prevalence. Data in Table 1 show malarial prevalence is positively correlated with sample size (Spearman correlation, $r_s = 0.56$, $P < 0.01$). Also, a significant

difference in sample size exists for islands scored with 0, 1, or 2 species of *Plasmodium* (Kruskal-Wallis test, $P < 0.05$). The three islands with largest samples had two species of *Plasmodium* detected, and the four islands with the smallest samples had no detected malaria. This pattern results at least in part from our collecting most heavily on islands where preliminary sampling revealed high prevalence of both species of *Plasmodium* (Saba, St. Christopher, St. Martin, Puerto Rico). (This detailed sampling was done as part of other studies on the population biology of the parasites.) When these few islands with sample sizes > 250 are removed from the analysis, the correlation between prevalence and sample size vanishes ($P > 0.05$).

On islands with parasite prevalence typical for anole populations, a small sample reveals the actual prevalence and species of parasite present. For example, in the first survey on Saba, only 43 lizards were collected, but both species of *Plasmodium* were found and in an overall prevalence very similar to the result of the much larger sampling (37% vs. 47%). Two samples were taken on St. Christopher, approximately 2 years apart, that differed in sample size (79 vs. 211) with no significant difference in prevalence (Staats and Schall 1996). It is possible that the prevalence of infection was low on some islands with small sample sizes, and any blood parasites there could have been missed in the sampling. However, chronic low parasite prevalence should not have had an effect on the evolution of showy traits in males; that is, low prevalence would be equivalent to zero prevalence. Nonetheless, the analysis below will correct for any possible bias of number of parasite species by sample size.

We compare color class of dorsal surface and dewlap by parasite burden in two ways. First, Kruskal-Wallis tests examine dorsal and dewlap color classes by percent of lizards infected with *Plasmodium*, haemogregarines, or intestinal helminths. None of the comparisons were significant ($P_s = 0.367 - 0.938$). Second, the number of species of *Plasmodium* and number of species of helminths were compared with color class. Sample sizes (number of populations) were too small for any kind of matrix test of our color classes and number of species. Therefore, we combined number of species into two levels, and color classes into two groups. To eliminate any subjective bias in joining color classes, we ran Fisher exact tests with every possible combination of color classes. Again, no significant association was observed ($P_s > 0.10$). This series of analyses was repeated using only populations with sample size > 99 , again with no significant results ($P_s > 0.10$). We conclude that there is a lack of association of color class and parasite burden.

Examination of the consensus phylogeny of anoles in the eastern Caribbean (presented in Roughgarden 1995) reveals all but one of the species of *Anolis* used here fall into one of three species groups, one found on Puerto Rico (the *crisatellus* group), one in the northern Lesser Antilles (the *bimaculatus* group), and one in the southern islands (*roquet* group). These species groups are in-

Table 1 Data on parasite loads and two showy traits (color of dorsal surface and dewlap color) in male anoles for 29 *Anolis* populations from 17 islands in the Caribbean. Given are island name, species of *Anolis* (and subspecies when appropriate), species group to which populations in the northern and eastern Caribbean belong (*B* bimaculatus, *R* roquet, *C* cristatellus), number of sites sampled on each island, scores for dorsal and dewlap color pattern, and prevalence (and number of species) of *Plasmodium*, haemogregarine, and helminth infections for each of the population of anoles

Island	<i>Anolis</i> Species	No. of sites	<i>n</i>	Dorsal score	Dewlap score	<i>Plasmodium</i> % Infected (no. species)	Haemogreg. % Infected	Helminths % Infected (no. species)
Anguilla	<i>A. gingivinus</i> (B)	4	97	1	3	7 (1)	0	22 (2)
St. Martin	<i>A. gingivinus</i> (B)	17	828	1	3	25 (2)	6	65 (3)
	<i>A. pogus</i> (B)	10	206	4	1	2 (1)	1	44 (1)
St. Bartélémy	<i>A. gingivinus</i> (B)	5	133	1	3	7 (1)	3	
Saba	<i>A. sabaanus</i> (B)	50	2086	3	3	47 (2)	6	76 (3)
St. Eustatius	<i>A. b. bimaculatus</i> (B)	6	78	4	4	0	0	45 (3)
	<i>A. schwartzi</i> (B)	4	48	3	2	0	0	50 (5)
St. Christopher	<i>A. b. bimaculatus</i> (B)	5	290	4	4	14 (2)	2	
	<i>A. schwartzi</i> (B)	5	16	3	2	0	0	
Antigua	<i>A. b. leachi</i> (B)	4	22	4	4	0	9	75 (7)
	<i>A. wattsi</i> (B)	4	13	3	2	0	0	62 (4)
Montserrat	<i>A. lividus</i> (B)	3	63	3	2	10 (1)	0	67 (5)
Dominica	<i>A. o. oculatus</i> (B)	3	62	3	2	13 (1)	2	
	<i>A. o. cabritensis</i>	2	72	4	2	12 (1)	11	
	<i>A. o. montanus</i>	1	46	4	3	0	0	
	<i>A. o. winstoni</i>	2	80	3	2	10 (1)	4	
Martinique	<i>A. roquet summus</i> (R)	6	161	4	3	4 (1)	9	
St. Lucia	<i>A. luciae</i> (R)	3	119	2	2	0	64	
St. Vincent	<i>A. trinitatis</i> (R)	4	79	2	2	13 (1)	<1	
Barbados	<i>A. extremus</i> (R)	2	28	4	3	0	0	
Grenada	<i>A. richardi</i> (R)	3	20	3	3	2 (1)	15	
	<i>A. aeneus</i> (R)	3	26	3	3	8 (1)	11	
Aruba	<i>A. lineatus</i>	3	83	3	4	0	0	
Curaçao	<i>A. lineatus</i>	3	15	3	4	0	0	
Puerto Rico	<i>A. evermanni</i> (C)	4	386	2	2	1 (1)	<1	
	<i>A. gundlachi</i> (C)	4	1516	1	3	22 (2)	<1	
	<i>A. stratulus</i> (C)	4	256	1	3	1 (1)	0	
	<i>A. cristatellus</i> (C)	1	216	1	3	1 (1)	2	
	<i>A. krugi</i> (C)	5	47	3	2	1 (1)	4	

indicated in Table 1. If color class or parasite burden is associated with phylogenetic history of the species, then each clade must be examined separately. The three species groups did not differ in parasite prevalence (Kruskal-Wallis test, $P = 0.40$). Color scores differ among the three species groups: 4/5 populations of the cristatellus group fall into color classes 1 and 2, whereas 11/12 bimaculatus and 4/6 roquet populations fall into classes 3 and 4 for dorsal color. The dewlap scores are similar among the species groups. Therefore, we next compare dorsal color vs. parasite load for the three groups. Percent of lizards infected with *Plasmodium* or haemogregarines did not differ among color classes for any of the species groups (Kruskal-Wallis tests, $P_s = 0.264-0.716$). Again, we conclude that there is no association of parasite load with color class.

Discussion

Two general predictions emerge from the Hamilton-Zuk hypothesis: (1) within populations of a showy species, the conspicuous ornament will be less showy in infected males; and (2) among species, those that have been infected with more parasites over their evolutionary his-

tory will be more showy. Both of these predictions have been subjected to scrutiny.

Within-population tests of the Hamilton-Zuk hypothesis have provided conflicting and paradoxical results. A detailed study by Møller (1994) found that the elongated tail feathers of male barn swallows are altered by parasitic infection. Resistance to infection appears heritable, and females prefer males with tail feathers in good condition. Thus, the hypothesis was strongly supported by Møller's study. Many other studies find a deleterious effect on a showy trait or extravagant behavior associated with parasitic infection. These include: guarding behavior of crickets (Simmons 1990), color of guppies (Houde and Torio 1992), display rate in guppies (Kennedy et al. 1987), holding a bower in satin bowerbirds (Borgia 1986), colors of redwing blackbirds (Weatherhead 1990) and jungle fowl (Zuk et al. 1990), and spermatophore production by crickets (Zuk 1987). Whereas some studies find a decrease in mating success by parasitized males (Jaenike 1988), others detect no reduction in mating success associated with a pathogen (Weatherhead 1990). More damaging to the hypothesis is the finding that parasitic infection in some species may lead to an increase in the showiness of males (directly contrary to the prediction emerging from the hypoth-

esis). Such paradoxical results were found for studies of wild zebra finches (*Taeniopygia guttata*) in Australia (Burley et al. 1991), whiptail lizards (*Cnemidophorus arubensis*) of Aruba island in the southern Caribbean (Schall 1986), and fence lizards (*Sceloporus occidentalis*) in California (Ressel and Schall 1989).

The among-population tests have also produced conflicting results. Supporting the hypothesis have been studies on the birds of North America and Europe (Hamilton and Zuk 1982; Read 1987), South America (Zuk 1991), and New Guinea (Pruett-Jones et al. 1991). The association of bright colors and parasite load is stronger in nonmigratory neotropical birds, compared with migratory species, perhaps because of their life-long contact with the same set of parasites (Zuk 1991). Ward (1988) found a positive association between parasite diversity and male color in his study of British fish. Other studies have found no relationship between parasite load and showy traits in lizards (Lefcort and Blaustein 1991), North American fish (Chandler and Cabana 1991), and in the complexity of bird song (Read and Weary 1990). Reexamination of the data for North American birds (Read and Harvey 1989) and British fish (Chandler and Cabana 1991) cast doubt on the previously described positive association between bright colors and parasite loads.

All of the previous among-species tests of the Hamilton-Zuk hypothesis have failed to meet one to all of the benchmarks listed by various critics and reviewed above. In our study we sought to confront these shortcomings. The data set included information on the color typical of each population of anoles as well as two measures of parasite load (number of parasite species and their prevalence). We sampled over the entire range of the population on the Lesser Antilles (the island or portion of the island for distinct subspecies). The parasites and hosts most likely have had a long coevolutionary association. We did not rank the colors by any measure of showiness, but instead simply cast each population of lizards into one of several distinct color classes. At least one taxon of parasite we examined (*Plasmodium*) harms lizards and can change the color of males. All of the populations of lizards are congeners, and the phylogeny of these species is well understood. An among-species test of the Hamilton-Zuk hypothesis predicts that lizards in different color classes should differ in parasite load. In this study, no hint emerged of the pattern predicted by the hypothesis.

Use of clearly defined color classes was our attempt to remove subjectivity from rankings of showiness in the lizards' color. Critics might argue that substantial information was lost and that a human subjective rating of showiness is still valuable in this kind of study. In this case, the conclusion drawn above remains if we subjectively compare populations of anoles that look extravagant to the human eye with those that appear drab. For example, some of the populations that in our opinion were least showy carried high parasite loads, such as *A. gingivinus* on St. Martin and *A. gundlachi* on

Puerto Rico. These lizards appear a drab, cryptic mottled brown color. Some very showy species, such as *A. bimaculatus* on St. Christopher and *A. sabanus* on Saba, also were heavily parasitized. Populations with low parasite loads included the dull *A. cristatellus* on Puerto Rico (which is very similar in appearance to *A. gundlachi*) and the showy *A. pogus* on St. Martin. On Dominica, the subspecies of *A. oculatus* that is most showy to the human eye, *A. o. muntanus*, was not infected with any blood parasite, whereas the other subspecies that varied from dull to showy all had about the same parasite burdens. The most complex dewlap among all the anole populations is carried by *A. lineatus* from Aruba and Curaçao. It was scored a 4 for its mix of colors, but also was unusual because it was asymmetrical on left and right sides, showing more bright orange on one side and yellow on the other. Nonetheless, neither population of *A. lineatus* was infected with any blood parasite. The most heavily parasitized species, *A. sabanus* from Saba island, displays a uniform pale yellow or orange dewlap that appears far less showy than the dewlap of *A. lineatus*.

What explains the disparate results of the among-species tests of the Hamilton-Zuk hypothesis? Pruett-Jones et al. (1991) noted that a pattern supporting the hypothesis exists for birds only when a broad taxonomic sweep of an entire region's avifauna is used in the analysis. The pattern is not seen when individual families of birds are studied. Also, as shown here, the pattern is not found for other vertebrate taxa. For example, both of the among-species studies involving lizards, Lefcort and Blaustein (1991) who studied 26 species among 8 families, and this study of anoles in the Caribbean, do not support the Hamilton-Zuk hypothesis (also, recall that the two within-population tests involving lizards came to paradoxical results). These results suggest some intriguing possibilities. Perhaps sexual selection works differently on birds than some other vertebrate taxa, or perhaps the pattern seen in the among-family studies shows a more ancient evolutionary interaction between birds and their parasites. The theoretical studies of Clayton et al. (1992) show that the outcome of interaction of parasites and the sexual selection of their hosts is strongly dependent on the specific kind of interaction between parasite and host.

In any case, the role of parasites in the behavior and ecology of their hosts was too long ignored by evolutionary ecologists. Parasites may not present the spectacle seen when a predator attacks its prey, but pathogens work relentlessly on every species of free-living animal. The Hamilton-Zuk hypothesis is now viewed as a landmark (Sheldon and Verhulst 1996) that continues to provoke discussion; it may well be among the most hotly debated ideas in behavioral ecology over the past decade. The hypothesis was ambitious because it attempted to resolve a century-old problem in evolutionary ecology by linking the pervasive influence of parasites with sexual selection. Whatever the outcome of testing of the hypothesis, the controversy has properly

led to a growing interest in how parasites influence host behavior, morphology, and physiology.

Acknowledgements We thank the people of the Caribbean islands for their warm welcome and understanding as we captured lizards around woodlands, farms, and homes. The van't Hof-Cornet family hosted us on Saba, and the staff of the El Verde Field Station assisted us on Puerto Rico. Our good natured field assistants were T. Bartolotta, M. Kaplan, R. Kim, M. McKnight, H. Jacumen, S. Vogt, W. Lichtenbelt, and R. Schall, and in the laboratory we called upon S. Osgood and S. Vogt. The research was funded by the National Geographic Society.

References

- Andersson MB (1994) Sexual selection. Princeton University Press, Princeton
- Borgia G (1986) Satin bowerbird parasites: a test of the bright male hypothesis. *Behav Ecol Sociobiol* 19:355–358
- Burley N, Tidemann SC, Halupka K (1991) Colour and parasite levels of zebra finches. In: Loye JE, Zuk M (eds) Bird parasite interactions. Oxford University Press, Oxford, pp 359–376
- Chandler M, Cabana G (1991) Sexual dichromatism in North American fresh water fish: do parasites play a role? *Oikos* 60:322–328
- Clayton DH (1991) The influence of parasites on host sexual selection. *Parasitol Today* 7:329–334
- Clayton DH, Pruett-Jones SG, Lande R (1992) Reappraisal of the interspecific prediction of parasite-mediated sexual selection: opportunity knocks. *J Theor Biol* 157:95–108
- Cox FEG (1989) Parasites and sexual selection. *Nature* 341:289
- Dobson AP, Pacala SV, Roughgarden JD, Carper ER, Harris EA (1992) The parasites of *Anolis* lizards in the northern Lesser Antilles. I. Patterns of distribution and abundance. *Oecologia* 91:110–117
- Dunlap KD, Schall JJ (1995) Hormonal alterations and reproductive inhibition in fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite *Plasmodium mexicanum*. *Physiol Zool* 68:608–621
- Fleishman LJ, Lowe ER, Leal M (1993) Ultraviolet vision in lizards. *Nature* 365:397
- Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387
- Houde AE, Torio AJ (1992) Effect of parasitic infection on male color pattern and female choice in guppies. *Behav Ecol* 4:346–351
- Jaenike J (1988) Parasitism and male mating success in *Drosophila testacea*. *Am Nat* 131:774–780
- Kennedy CEJ, Endler JA, Poynton SL, McMinn H (1987) Parasite load predicts mate choice in guppies. *Behav Ecol Sociobiol* 21:291–295
- Lazell JD (1972) The anoles (Sauria, Iguanidae) of the Lesser Antilles. *Bull Mus Comp Zool Harvard* 143:1–115
- Lefcort H, Blaustein AR (1991) Parasite load and brightness in lizards: an interspecific test of the Hamilton-Zuk hypothesis. *J Zool Lond* 224:491–499
- Merila J, Bjorklund M, Bennett GF (1995) Geographic and individual variation in haematozoan infections in the greenfinch, *Carduelis chloris*. *Can J Zool* 73:1798–1804
- Møller AP (1990) Parasites and sexual selection: current status of the Hamilton and Zuk hypothesis. *J Evol Biol* 3:319–328
- Møller AP (1994) Sexual selection and the barn swallow. Oxford University Press, Oxford
- Pomiankowski A (1987) The costs of choice in sexual selection. *J Theor Biol* 128:195–218
- Pruett-Jones SG, Pruett-Jones MA, Jones HI (1991) Parasites and sexual selection in a New Guinea avifauna. *Curr Ornithol* 8:213–245
- Read AF (1987) Comparative evidence supports the Hamilton and Zuk hypothesis on parasites and sexual selection. *Nature* 328:68–70
- Read AF (1990) Parasites and the evolution of host sexual behaviour. In: Barnard CJ, Harvey PH (eds) Parasitism and host behaviour. Taylor and Francis, London, pp 117–157
- Read AF, Harvey PH (1989) Reassessment of comparative evidence for Hamilton Zuk theory on the evolution of secondary sexual characters. *Nature* 339:618–620
- Read AF, Weary DM (1990) Sexual selection and the evolution of bird song: a test of the Hamilton-Zuk hypothesis. *Behav Ecol Sociobiol* 26:47–56
- Ressel S, Schall JJ (1989) Parasites and showy males: Malarial infection and color variation in fence lizards. *Oecologia* 78:158–164
- Roughgarden J (1995) *Anolis* lizards of the Caribbean. Oxford University Press, Oxford
- Ryan MJ, Keddy-Hector A (1992) Directional patterns of female choice and the role of sensory biases. *Am Nat* 139:S4–S35
- Schall JJ (1986) Prevalence and virulence of a haemogregarine parasite of the Aruban whiptail lizard, *Cnemidophorus arubensis*. *J Herpetol* 20:318–324
- Schall JJ (1996) Malarial parasites of lizards: diversity and ecology. *Adv Parasitol* 37:255–333
- Schall JJ, Bromwich CR (1994) Interspecific interactions tested: two species of malarial parasite in a West African lizard. *Oecologia* 97:326–332
- Schall JJ, Vogt SP (1993) Distribution of malaria in *Anolis* lizards of the Luquillo Forest, Puerto Rico: implications for host community ecology. *Biotropica* 25:229–235
- Sheldon BC, Verhulst S (1996) Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends Ecol Evol* 11:317–321
- Simmons LW (1990) Post-copulatory guarding, female choice, and the levels of gregarine infections in the field cricket, *Gryllus bimaculatus*. *Behav Ecol Sociobiol* 26:403–407
- Staats CM, Schall JJ (1996) Malarial parasites (*Plasmodium*) of *Anolis* lizards: biogeography in the Lesser Antilles. *Biotropica* 28:388–393
- Ward PI (1988) Sexual dichromatism and parasitism in British and Irish freshwater fish. *Anim Behav* 36:1210–1215
- Weatherhead PJ (1990) Secondary sexual traits, parasites, and polygyny in red-winged blackbirds, *Agelaius phoeniceus*. *Behav Ecol* 1:125–130
- Weatherhead PJ, Bennett GF (1991) Ecology of red-winged blackbirds parasitism by haematzoa. *Can J Zool* 69:2352–2359
- Weatherhead PJ, Bennett GF (1992) Ecology of parasitism of brown-headed cowbirds by haematzoa. *Can J Zool* 70:1–7
- Weatherhead PJ, Bennett GF, Shutler D (1991) Sexual selection and parasites in wood-warblers. *Auk* 108:147–152
- Zuk M (1987) The effects of gregarine parasites, body size, and time of day on spermatophore production and sexual selection in field crickets. *Behav Ecol Sociobiol* 21:65–72
- Zuk M (1991) Parasites and bright birds: new data and a new prediction. In: Loye JE, Zuk M (eds) Bird-parasite interactions. Oxford University Press, Oxford, pp 317–327
- Zuk M, Johnson K, Thornhill R, Lignon JD (1990) Parasites and male ornaments in free-ranging and captive red jungle fowl. *Behaviour* 114:232–248