

# Evolution and Maintenance of Social Status-Signaling Badges

## Experimental Manipulations in Lizards

**Martin J. Whiting, Kenneth A. Nagy, and Philip W. Bateman**

Sexual selection theory aims to explain the evolution of extravagant traits that should seemingly impose a survival cost on the bearer (reviewed in Andersson [1994] and Andersson and Iwasa [1996]). This paradox is normally explained as a trade-off between reproductive success and survival. Two processes are thought to drive the evolution of extravagant traits: male contest competition and female choice (Andersson 1994). Traits that function in female choice are referred to as ornaments, while weapons and signals used in male contest competition are called *armaments* (Berglund, Bisazza, and Pilastro 1996). There is also increasing evidence that armaments frequently function in both aggressive interactions between males and directly in female choice (Kodric-Brown and Brown 1984; Moller 1988a; see Johnstone and Norris [1993] for a theoretical treatment; Morris, Mussel, and Ryan 1995; reviewed in Berglund, Bisazza, and Pilastro [1996]; Beani and Turillazzi 1999). Alternatively, successful males with large armaments may have a higher reproductive success as a result of competitive exclusion (e.g., *Lacerta agilis*, Olsson 1994a). Furthermore, animal signaling is complex and often consists of multiple signals (Moller and Porniankowski 1993; Johnstone 1995a, 1996, 1997) and sometimes multiple ornaments that exploit different preferences, but with the same ultimate function (Brooks and Couldridge 1999). Signaling is further complicated by competition among signalers on information transfer during communication, motivational state, information content and reliability, the signaling environment, the receiver's sensory system, receiver psychology, predation risk, phylogenetic constraints, and a myriad of other factors (Fleishman 1986, 1988a, b, c, 1992; Ryan et al. 1990; Guilford and Dawkins 1991; Endler 1992, 1993; Arak and Enquist 1993; Dawkins 1993; McGregor 1993; Ryan and Rand 1993, 1995; Endler and Houde 1995; Godfray 1995; Greenfield 1997; Johnstone 1997; Leal and Rodriguez-Robles 1997; Zuk and Kolluru 1998; Leal 1999). Disentangling these various factors, searching for common patterns in diverse systems, and marrying empirical work with current signaling theory will be a challenge for some time to come. Furthermore, to properly understand signal design and evolution, we need to make use of many different biological disciplines (see Endler 1993) and even other scientific disciplines such as physics.

Animal signals have been the subject of intense study for the last two decades, increasingly so by modelers. As Grafen and Johnstone (1993) so succinctly point out, ESS (evolutionarily stable strategy) models of biological signaling are useful because they are explicit, more likely to be error-free, and allow more complicated exploration of the assumption of evolutionary stability. Recent work on signal terminology and concepts (Dawkins and Guilford 1991; Dawkins 1993; Guilford and Dawkins 1995; Maynard Smith and Harper 1995) and formal mathematical models (e.g., Grafen 1990; Getty 1998) have resulted in a framework in which signal content, reliability, and evolution can be examined. Animal communication biology has therefore entered an exciting new era in which theoretical models can be empirically tested. One branch of communication biology in which such interchange is potentially highly rewarding is the study of dominance disputes between males (status signaling or the badges-of-dominance game in particular) (Dawkins and Krebs 1978; Maynard Smith and Harper 1988; Kim 1995). Many animals possess markings (generally color patches) or features (e.g., lizard tails) that function as badges of status (Fox, Heger, and DeLay 1990; Krebs and Davies 1993). The term *badges of status* was coined for arbitrary structures (such as a color patch) that convey status signals and are uncostly to produce and potentially open to cheating (Dawkins and Krebs 1978; Roper 1986). Conversely, armaments such as antlers play a direct role in settling a contest, conferring a true advantage to the bearer (Senar 1999). When producing a badge does incur a cost, it may be argued that badges are no more than ordinary handicaps. It is also important to separate production from maintenance costs (e.g., Veiga and Puerta 1996).

According to the badges-of-status hypothesis, frequency- dependent selection maintains honest signaling of aggressiveness (Maynard Smith and Harper 1988). Alternatively, Rohwer (1982) proposed negative frequency-dependent selection to explain two badge-associated strategies in birds-dominants and subordinates-which are equally fit. The idea is that the two strategies are a form of resource exploitation that results either in cooperative exploitation (e.g., mutually beneficial foraging strategies in Harris' sparrows) or in alternative reproductive strategies.

Status signaling occurs in such diverse taxa as insects (Greenfield and Minckley 1993; Beani and Turillazzi 1999), fish (Wickler 1957 in Dawkins and Krebs 1978; de Boer 1980; Zimmerer and Kallman 1988; Morris, Mussel, and Ryan 1995), frogs (Davies and Halliday 1978; Arak 1983b), lizards (Fox, Heger, and DeLay 1990; Thompson and Moore 1991b; Olsson 1994a, b; Zucker 1994a, b; Carpenter 1995a, b), birds (e.g., Rohwer 1975, 1977, 1982; Rohwer and Rohwer 1978; Studd and Robertson 1985a; Moller 1987b; Whitfield 1987; Senar et al. 1993,2000; Furlow, Kimball, and Marshall 1998; Senar and Camerino 1998; Senar 1999), and mammals (Clutton-Brock and Albon 1979) (see also Table 2 - 1). In the case of some mammals, birds, and frogs, status is frequently conveyed vocally (reviewed in Andersson [1994]; Leonard and Horn 1995). Also, in some species, individuals may have more than one armament that functions as a status-signaling badge (e.g., for tree lizards, see Zucker [1994a]; for birds, see Balph, Balph, and Romesburg [1979]). Status-signaling badges signal dominance and/or fighting ability and thereby prevent or reduce the costs of fighting (Rohwer 1975). However, badges may also signal aggressiveness (Rohwer 1982; Studd and Robertson 1985a, b; Maynard Smith and Harper 1988; Johnstone and Norris 1993). Aggressiveness may not be tightly linked to size or strength such that badges may be used to settle disputes over less valuable resources, whereas fighting ability is used in disputes over more valuable resources (Maynard Smith 1982; Maynard Smith and Harper 1988; Johnstone and Norris 1993). In addition, contests are more likely to escalate to fights between males of similar aggressiveness (Maynard Smith and Harper 1988). By using badges in asymmetric contests, individuals can avoid unnecessary energy expenditure and increased risk of injury or predation involved in fighting assessment (Rohwer 1982). Badges are most effective in quickly resolving conflicts when "large" asymmetries exist (Maynard Smith and Harper 1988); this is also predicted by the sequential assessment game (Enquist et al. 1990).

Status signaling is well known for its role in dominance disputes during the reproductive season in which the outcome determines access to mates. However, in nonbreeding, flocking birds, status signaling that determines access to food occurs in all age-sex classes (Rohwer 1975, 1977; partial review in Roper [1986]; Moller 1987b; reviewed in Whitfield [1987]); although the results of some previous studies are increasingly being challenged (e.g., Whitfield 1987; Wilson 1992; Slotow, Alcock, and Rothstein 1993), while other studies have failed to find support for the status signaling hypothesis (SSH) as an explanation for plumage variability (reviewed in Whitfield [1987] and Maynard Smith and Harper [1988]). An increasingly recognized alternative to the SSH is the individual recognition hypothesis (Whitfield 1986, 1987, 1988), although both may occur simultaneously in the same population (Whitfield 1987).

In general, contests between males are settled through ritualized displays in which the dominance status of the signaler is transmitted to the receiver (Enquist and Leimar 1983; Kim 1995). The signal itself can take many forms (Johnstone 1996, 1997), but the intended purpose is common to all taxa: transmit information about dominance and/or fighting ability/aggressiveness, thereby avoiding or reducing the costs of fights with a predictable outcome (Maynard Smith 1982). The information content and honesty of the signal may, of course, vary greatly (Dawkins and Guilford 1991; Semple and McComb 1996).

There are two types of signals in agonistic communication: performance and strategic (Hurd 1997a). Performance signals are also referred to as unambiguous/assessment signals (Maynard Smith and Parker 1976; Maynard Smith 1982; Maynard Smith and Harper 1988) and condition-dependent handicaps (Grafen 1990).

Performance signals are in essence, unbluffable. For example, in many cichlids, fighting ability is tightly linked to size. An early stage of sequential assessment is lateral displaying, in which cichlids pose side on with an opponent and smaller individuals will always appear smaller (Hurd 1997b). Conversely, all individuals are capable of making strategic signals (conventional signals, *sensu* Dawkins 1993), and these can all be bluffed or exaggerated to some degree (Hurd 1997a). (Badges of status are therefore conventional signals [Dawkins 1993]). Numerous game-theory models have attempted to formalize signaling strategies in contests (e.g., Enquist 1985; Maynard Smith and Harper 1988; Grafen 1990; Grafen and Johnstone 1993; Johnstone and Grafen 1993; Johnstone and Norris 1993; Kim 1995; Getty 1998; Szamado 2000). This has resulted in a framework in which to examine the evolution and maintenance of signaling systems and has set the stage for empirical testing of signaling theory in a variety of taxa.

## **Maintenance of Signaling System Stability**

The last decade has seen a concerted attempt to understand signal-receiver coevolution and the selective forces underlying signal evolution (Ryan et al. 1990; Endler 1992, 1993; Arak and Enquist 1993; Dawkins 1993; Grafen and Johnstone 1993; Ryan and Rand 1993, 1995; Morris and Ryan 1996). Guilford and Dawkins (1991) proposed that signal design consists of two components: strategic design and efficacy. *Strategic design* refers to how a signal is designed by natural selection to ensure information transfer and a corresponding reaction from the receiver. Efficacy refers to the manner in which the information is transferred, such that it is easily measured by the receiver. Signals may be favored by natural selection if they are energetically cheap, effectively manipulate the receiver, and reduce the risk of predation (Johnstone 1997).

Signals may also be costly (reviewed in Zuk and Kolluru [1998]). For example, frog calls attract predators (Tuttle and Ryan 1981). The exact mechanisms driving the evolution and maintenance of badges are controversial. Possible mechanisms include natural selection (Rohwer 1975, 1982); sexual selection (Olsson 1994a); both acting simultaneously (Moller 1988a); and other less clear forms of selection, such as mimicry (reviewed in Andersson [1994]). However, it is now accepted that signal systems are complex and not always assignable to general selective pressures (Dawkins 1993; Greenfield 1997).

Occasional deception need not disrupt the signaling system provided that signals are on average honest (Johnstone and Grafen 1993). If signals were not honest, deception would ultimately result in an unresponsive receiver, and the system would become redundant (Johnstone 1997; but see Szamado [2000]). This is one of the most challenging areas in communication biology: the stability of signal systems and barriers to cheating (if any). Signals can vary greatly in their information content and honesty/reliability (Dawkins and Krebs 1978; Krebs and Dawkins 1984; Dawkins and Guilford 1991; Semple and McComb 1996; Viljugrein 1997). A major theoretical contribution to this area is the handicap principle, originally conceived by Zahavi (1975, 1977) and later formalized by Grafen (1990) (but also see Getty [1998]). There are two theoretical interpretations of this principle. The "strategic handicap" interpretation suggests that for maintenance of honesty, there must be a cost associated with the signal such that it only pays high-quality (or highly motivated) (Enquist 1985) individuals to make costly signals. In this "quality-dependent" interpretation (most commonly referred to as condition dependent), the benefits outweigh the costs only for superior individuals, such that selection favors quality-dependent expression of traits. (Both models are reviewed in Johnstone [1995b].)

**Table 2-1 Studies of status signaling that have in some way examined costs associated with signaling.** Many studies did not explicitly test constraints to honest signaling, but the results provided correlative evidence or refuted specific handicap-based models. This table provides evidence for costly signaling (if any), how cheating is constrained, and any comments/ambiguities from the studies that may warrant further investigation; we included only those studies that referred specifically to status-signaling badges or those that dealt with an animal's status in the context of signalling/dominance costs since 1975. There are many other studies in which dominance and aggression were examined in a cost-benefit analysis, similar to status signaling. EA = experiment under artificial conditions (e.g., in aviaries); EF = experiment performed in the field; OF ~ observations in the field; OA = observed under artificial conditions (If measurements were made [e.g., metabolic rate] but nothing [e.g., animal's phenotype, diet, or potential for interaction] was manipulated, a study was scored as observation based, whether in the laboratory or field.)

Species	Type of Study	Evidence for a Badge/Signal Cost	Constraints to Cheating	Comments/Ambiguities	Reference
<b>Arthropods</b>					
Tarbrush grasshopper ( <i>Liguroteffix planum</i> )	OF, EF	Speculative	Likely morphological and physiological	Calling rate and number of shucks/calf indicated fighting ability. High rate and call complexity should constrain cheating.	Greenfield and Minckley (1993)
Stenogastrine wasp ( <i>Parischnogaster mellyi</i> )	EA	Yes	Social control	Males with manipulated badge (extra stripes) were challenged more frequently than controls.	Beani and Turillazzi (1999)
<b>Amphibians</b>					
Common toad ( <i>Bufo bufo</i> )	OF, EA	No	Morphology	Call frequency was anatomically constrained: larger males had a larger larynx = deeper croak.	Davies and Halliday (1978)
<b>Fish</b>					
Siamese fighting fish ( <i>Betta splendens</i> )	EA	Yes	Energetic cost	No badge as such; fighting ability was signaled during ritualized aggression.	Halperin et al. (1998)
Miclas cichlid ( <i>Cichlasoma citrinellum</i> )	EA	Yes	Energetic cost	No badge as such; aggression (not fighting ability) was signaled during rituals.	Barlow, Rogers, and Fraley (1986)
Firemouth cichlid ( <i>Cichlasoma meeki</i> )	EA	Yes	Carotenoids	Red area on ventral surface displayed during aggressive interactions was dependent on amount of carotenoids in diet.	Evans and Norris (1996)
<b>Lizards</b>					
Sand lizard ( <i>Lacerta agifis</i> )	EA, OF	Yes	Resource allocation social control?	A trade-off existed between somatic growth and badge size. Social control hypothesis requires testing.	Olsson (1994b); Olsson and Silverin (1997)

Table 2-1 (Continued)

Species	Type of Study	Evidence for a Badge/Signal Cost	Constraints to Cheating	Comments/Ambiguities	References
Tree lizard ( <i>Urosaurus ornatus</i> )	(1) EA	No	Suggest that system is a mixed ESS	A good argument is provided to support his assertion.	Thompson and Moore (1991b)
	(2) EA	Speculative	Suggested costs: predation and/or increased thermal load	Signaling costs were not explicitly tested.	Zucker (1994a)
Mediterranean lizard ( <i>Psammodromus algirus</i> )	EA	Yes	Social control	Small males with painted heads were attacked by larger males.	Martin and Forsman (1999)
Augrabies flat lizard ( <i>Platysaurus broadleyi</i> )	OF	Yes (correlative)	Metabolic cost	—	Whiting et al. (this study)
<b>Birds</b>					
Dark-eyed junco ( <i>Junco hyemalis</i> )	EA	No	—	Failed to support incongruence hypothesis.	Holberton, Able, and Wingfield (1989)
	OA	No	Constraints discussed in general terms with reference to Rohwer's work	Weak support for status signaling; most likely via learned association (e.g., between plumage and	
Collared flycatcher ( <i>Ficedula albicollis</i> )	EF	Yes (correlative)	Social control and cost of parental care	—	Qvarnstrom (1997)

Table 2-1 (Continued)

Species	Type of Study	Evidence for a Badge/Signal Cost	Constraints to Cheating	Comments/Ambiguities	References
Great tit ( <i>Parus major</i> )	(1) CA	Yes (correlative)	Metabolic cost	Heart weight (relative to body weight) was greater in more dominant males.	Roskaft et al. (1986)
	(2) EF, EA	No	—	Speculate that system may be a mixed ESS. Criticized by Wilson (1992).	Jarvi and Bakken (1984)
	(3) EA	Yes	Possibly incongruence hypothesis	Rejected social control hypothesis. Design/results were criticized by Wilson (1992) and Slotow, Alcock, and Rothstein (1993)	Jarvi Walso, and Bakken(1987)
	(4) E F	Speculative	—	Weak evidence was found for status signaling in females and none in males. Suggests badge may reflect history of risk and energetic costs associated with successful fighting history.	Wilson (1992)
Pied flycatcher ( <i>Ficedula hypoleuca</i> )	(1) OA	Yes (correlative)	Metabolic cost	Critical of above studies; little support for bright plumage functioning as badge.	Roskaft et al. (1986) Huhta and Alatalo (1993)
	(2) EF	No			
	(3) OF	Yes (correlative)	Predation	—	Slagsvold, Dale, and Kruszewicz (1995)
House sparrow ( <i>Passer domesticus</i> )	(1) EA	Yes	Social control	Slotow, Alcock, and Rothstein (1993) questioned whether plumage variation in house sparrows even signals social status.	Moller (1987a)
	(2) EF	Speculative	Survival disadvantage	Simulated cheaters had lower survival; no benefit for cheaters in terms of offspring fledged.	Veiga (1993, 1995)
	(3)--	Yes	—	Badge size was negatively correlated to health; badge size was an honest signal of condition.	Moller, Kimball, and Eritzoe (1996)

Table 2-1 (Continued)

Species	Type of Study	Evidence for a Badge/Signal Cost	Constraints to Cheating	Comments/Ambiguities	References
	(4) OA, OF	Yes	Diet/access to food	Greater access to food during molt positively correlated with badge size; juveniles were forced to use more blood proteins during molt due to poorer body condition.	Veiga and Puerta (1996)
	(5) EA	No	—	No support for social control hypothesis; low sample size/statistical power.	Solberg and Ringsby (1997)
	(6) OF	Yes	Endocrine-immunosuppressive trade-off	Breeding males with larger badges had lower, immunocompetence.	Gonzalez, Sorci, and de Lope (1999)
	(7) EA	No	—	Birds fed on protein-rich and protein-poor diets. Diet had no significant effect on size and spectral qualities of badge.	Gonzalez et al. (1999)
	(8) EA	Yes	Endocrine-immunosuppressive trade-off	Testosterone levels positively correlated with badge size; corticosterone reduced immunocompetence; relationship with testosterone uncertain.	Evans, Goldsmith, and Norris (2000); also see Poiani, Goldsmith, and Evans (2000)
Least auklets ( <i>Aethia pusilla</i> )	OF, EF	Speculative	Social control and/or predation	Signaling costs were not explicitly tested.	Jones (1990)
Willowtit ( <i>Parus montanus</i> )	OF	Yes (correlative)	Metabolic cost	Metabolic rate was related to dominance rank; badge size was not measured.	Hogstad (1987)
Yellow warbler ( <i>Dendroica petechia</i> )	EF, OF	No	Different but equally successful strategies adopted by different morphs	Appears to be a mixed ESS.	Studd and Robertson (1985a)
White-crowned sparrow (1) EF ( <i>Zonotrichia leucophrys</i> )		No	As above	No support was found for social control hypothesis.	Keys and Rothstein (1991)

Table 2-1 (Continued)

Species	Type of Study	Evidence for a Badge/Signal Cost	Constraints to Cheating	Comments/Ambiguities	References
	(2) EA	No	increased predation risk suggested as barrier to cheating	Rejected social control hypothesis.	Slotow, Alcock, and Rothstein (1993)
Harris' sparrow ( <i>Zonotrichia querreula</i> )	(1) EF	Yes	Social control	Design was criticized by Shields (1977)	Rohwer (1975, 1977)
	(2) EF	Yes	Incongruence hypothesis	—	Rohwer and Rohwer
	(3) EF	N/A	Frequency-dependent selection (shepherd hypothesis)	Dominants and subordinates coexist in a mutualistic relationship; equal fitness.	Rohwer and Ewald (1981), also see Rohwer (1982)
Domestic rooster ( <i>Gallus g. domesticus</i> )	(1) EA, OA	Yes (correlative)	Probably social control	—	Leonard and Horn (1995)
	(2) -	No	—	Hypothesis that crowing was energetically expensive (therefore preventing cheating) was rejected.	Horn, Leonard, and Weary (1995)
Red jungle fowl ( <i>Gallus gallus</i> )	OA	No	—	Crowing had a minimal energetic cost.	Chappell et al. (1995)
Scarlet-tufted malachite sunbird ( <i>Nectarinia johnstoni</i> )	OF	Yes	Uncertain	Traits were condition dependent; fluctuate with environmental conditions.	Evans (1991)
Ring-necked pheasant ( <i>Phasianus colchicus</i> )	EA	Yes	Social control	Social control of cheating was not explicitly mentioned, but like-versus-like aggression suggests this is the case.	Mateos and Carranza (1997)
Siskin ( <i>Carduelis spinus</i> )	OA	Yes	Stress	Subordinates had a higher metabolic rate due to stress-related encounters with dominants.	Senar et al. (2000)
<b>Mammals</b>					
Red deer ( <i>Cervus elephas</i> )	OF, EF	Speculative	Physiological: energetic cost to roaring	—	Clutton-Brock and Albon (1979)



Another interpretation is that signals are not costly because they are "uncheatable"; instead, costly signals have evolved to enhance a trait's expression and these are termed *revealing handicaps* (Iwasa, Pomiankowski, and Nee 1991). The handicap principle, in the context of honest signaling, has received much theoretical attention (thoroughly reviewed by Johnstone [1995b]). However, much of this attention has been skewed toward female choice.

Here, we review recent theoretical contributions to status signaling; in particular, we review by major taxonomic group studies that in some way deal with constraints to cheating (Table 2 - 1). We also examine the factors necessary to maintain an ESS in light of honest signaling theory (Table 2-2). We have excluded studies that merely demonstrate status signaling without regard to signaling constraints and include only studies published since 1975 (when Zahavi published his first treatment of the handicap principle).

## Signaling Costs

A central theme in discussions of status signaling is the issue of cheating (reviewed in Senar [1999]). Status-signaling badges (Dawkins and Krebs 1978) have been referred to as arbitrary indicators of social status (e.g., a color patch on a bird). In other words, badges are theoretically cheap to produce and they should therefore be easily mimicked. What, for example, prevents a low-ranking individual from assuming a dominant's badge? Clearly, cheating is minimal; otherwise, most signaling systems employing badges would be unstable and break down. Recent models (e.g., Johnstone and Grafen 1993; Johnstone and Norris 1993) support the notion that cheating occurs at a reduced level and have argued for contest-independent costs that exceed the costs of honest advertisement. For example, Veiga (1993) found that male house sparrows with experimentally enlarged badges acquired more nest sites but raised fewer offspring than control and badge-reduced males. Also, a follow-up study (Veiga 1995) showed reduced survival of yearling males with experimentally enlarged badges, suggesting a survival cost for cheaters. A number of costs have been proposed as constraints to cheating (reviewed in Table 2- 1) and these fall into two categories: those that are independent of actual contests and those that are paid during contests. We deal with contest independent costs first.

Elevated levels of androgens associated with aggression (e.g., testosterone) can be energetically costly (Marler et al. 1995) and also may compromise the immune system (Folstad and Karter 1992; Zuk, Johnsen, and Maclarty 1995; Moller, Kimball, and Erritzre 1996; Salvador et A 1997; Qvarnstrom and Forsgren 1998; Evans, Goldsmith, and Norris 2000; Poiani, Goldsmith, and Evans 2000). If badge size signals aggressiveness, it is reasonable that variation in the ability of individuals to bear this cost will exist (Johnstone and Norris 1993). Another physiological cost of dominance is a higher metabolic rate. More aggressive individuals have more frequent encounters with rivals, and this is mediated proximally through elevated hormone levels (Hogstad 1987). Increased metabolic rates correlating with dominance have been confirmed for pied flycatchers and great tits (Roskaft et al. 1986) and Willow tits (Hogstad 1987), while increased levels of testosterone resulted in an increase in social status in satin bowerbirds (Collis and Borgia 1992). Conversely, no significant relationship was found between social rank and androgens in dark-eyed juncos (Holberton, Able, and Wingfield 1989) and house finches (Belthoff, Dufty, and Gauthreaux 1994), and only a marginal relationship between metabolic rate and dominance was found for dippers (Bryant and Newton 1994).

**Table 2-2 Current theoretical models for maintenance of signaling systems, particularly as they apply to badges-of-status game.** Signaling systems fall into two general categories: costly and cost-free (Hurd 1997a). We have focused on formal mathematical models but have included some references (indicated by an asterisk) whose models are inferred, based on empirical work.

Model	Costly or Cost-Free?	Maintenance of Signal Reliability and ESS
Zahavi (1975*, 1977*) Pomiankowski (1987 Grafen (1990); Johnstone and Grafen (1993); Maynard Smith (1991)	Costly	The handicap principle: a signal's cost enforces its reliability. (Companion models suggest that cheating is permitted, but incidence must be low.)
Rohwer (1977*); Maynard Smith and Harper (1988)	Costly	Socially enforced: the "social control hypothesis."
Rohwer and Roh (1978*).	Costly	Incongruence hypothesis
Owens and Hartley (1991) (1) "Cheat" (2) "Trojan sparrow"	Costly Cost-free	Social control. In the absence of honest phenotypic limitations, the Trojan sparrow strategy can successfully invade honest populations. Result: mixed fighting strategies, badges-of-status model reduced to conventional hawk-dove model.
Dawkins and Guilford (1991)	Cost-free	Dependent on high cost of assessing signaler and low gain for extra information (to receiver). Occasional "probing" by receiver keeps cheating low.
Johnstone and Norris (1993)	Costly	A cost independent of a contest/ aggression.
Maynard Smith (1994)	Cost-free	Participants place the possible outcomes of an interaction in the same rank order.
Krakauer and Pagel (1995)	Cost-free	Constraints on population spatial structure.
Adams and Mesterton- Gibbons (1995)	Costly	At ESS, only weak and strong individuals threaten, not intermediates. Reason: although threatening is very risky for weak individuals, the pay-off is high.
Hurd (1997a) (1) Conventional signals	Cost-free	ESS is maintained by signaler's state. Weak individuals avoid provoking stronger individuals by signaling their strength; stronger individuals avoid escalated contests.
(2) Conventional signal + cost	Costly	Use of a handicapped signal is more likely to influence weaker individuals, for which the cost will be greater. Stronger individuals of higher fighting ability gain less by avoiding conflict (escalated contests).
Keys and Rothstein (1991*) Slotow Alcock, and Rothstein (1993) and references therein*; Slagsvold, Dale, and Kruszewicz (1995*)	Costly	Increased predation is associated with more conspicuous coloration.
Studd and Robertson (1985a*); Thompson and Moore (1991b*)	Cost-free	Mixed ESS: different morphs adopt different but equally successful reproductive strategies.

Few costs that are directly linked to badge size have been identified. One risk associated with conspicuous plumage frequently mentioned in the sexual selection literature is increased conspicuousness to predators (Olsson 1993b; Andersson 1994). In support of this, Slagsvold, Dale, and Kruszewicz (1995) reported higher predation on bright male pied flycatchers relative to drab (female-like) males in the breeding season. Other studies have cited predation as a possible constraint to badge size, but without quantitative support. These include studies on tree lizards, least auklets, and white-crowned sparrows (references in Table 2-1). The idea is that males are differentially vulnerable to predation such that only superior males can bear the cost (increased risk of predation) of a large badge (the handicap principle). It has been argued that in birds, males with larger bibs are unlikely to be significantly more conspicuous to predators (Senar 1999). Instead, it is more likely that dominant males are more active or exposed than subordinates (with smaller badges), and therefore more susceptible to predation (Veiga 1993). Furthermore, a recent study on nest defense in house sparrows showed that males with larger badges, in the presence of a mounted mustelid predator, performed more risky behavior. This is explained by an improving cost/benefit ratio because males with larger badges likely have greater confidence in their paternity (Reyer et al. 1998).

Deception in many bird taxa is socially controlled during contests (Table 2-1). Under the social control hypothesis, a subordinate individual bearing a dishonestly large badge will pay the full cost of cheating if challenged by a dominant individual bearing an honest badge (Maynard Smith and Harper 1988). Social control assumes like-versus-like aggression such that individuals of the same age and sex challenge each other (Maynard Smith and Harper 1988). Slotow, Alcock, and Rothstein (1993) criticize previous studies invoking social control of cheating and argue that like-versus-like aggression may not be sufficient to prevent deception if the benefits outweigh the costs and may instead be randomly directed. Furthermore, they evaluated all studies of birds testing the social control hypothesis and concluded that the evidence thus far (1993) was "tenuous." Some studies subsequent to that of Slotow, Alcock, and Rothstein (1993) have suggested social control of cheating (Table 2 - 1).

## Study Organism

The Augrabies flat lizard (Plate 1), *Platysaurus broadleyi* (formerly *Platysaurus capensis* [part]; Branch and Whiting [1997]), is a relatively small cordylid lizard (adult snout-vent length [SVL]: 64-84 mm) restricted to rocky terrain in the Gordonia-Kenhardt district of the Northern Cape Province, South Africa. At Augrabies Falls National Park, local populations are dense and large aggregations frequently occur along the Orange River in the presence of their primary prey, the black fly (*Simullum* spp.). Black flies occur in discrete plumes in the fast-flowing sections of the river, where conditions are most favorable for breeding. Consequently, the lizards have an extremely abundant food source and frequently occur in aggregations numbering in the hundreds. Males are territorial (Whiting 1999), although not all males defend territories, particularly in high-density areas where territories are at a premium (Whiting, unpublished data). As a result, the mating system appears to vary between a classical territorial system in which males offer the females no resources, to a resource defense polygyny in which males control areas with high prey abundance (Whiting, personal observation). In general, males approach many females but given a choice prefer larger females (Whiting and Bateman 1999).

In areas of high lizard abundance, the frequency of male-male interactions is high, but physical contests are generally avoided through the use of concealed badges of status that are flashed at rivals. Status-signaling badges in *P. broadleyi* are orange and/or yellow abdominal patches (Plate 2). The badge is bordered anteriorly by a black chest. The ventral surfaces of the thighs are also orange, as is a lateral stripe that generally extends about 30-40% of the distance between the front and hind limbs. The anterior edge of the lateral stripe matches the anterior edge of the ventral component of the badge. The orange ventral surface of the thighs and the lateral stripe may enhance the effect of the badge and serve as signal amplifiers (Hasson 1991; Plate 2). Males display their badge by raising one side of their body to an angle of 70-80°, such that a rival has a clear view of their

abdomen. This behavior is termed a *ventral display* (Plate 3) and may be performed from either a stationary position or while approaching a rival. Males also sometimes chase a rival either before or after a ventral display. Occasional disputes do result in fights, although infrequently and generally when a high-quality resource is disputed (Whiting, unpublished data) (Plate 4). It is currently unknown whether abdominal pigment production is costly in flat lizards. Therefore, for the purposes of this chapter, we refer to the colored abdominal patch as a badge.

Many factors influence contest success in lizards and territorial lizards in particular. These include residency/resource-holding power, body size, motivational state, and androgen levels (Cooper and Vitt 1987; Olsson 1992, 1993a; Marler et al. 1995; Tokarz 1995a). Residency in *P. broadleyi* is important for contest success; however, in high-density areas males have smaller territories or may not defend territories at all (Whiting, unpublished data). Males also are readily visible to observers and sufficiently habituated to humans to allow relatively close observation. *Platysaurus broadleyi* at Augrabies is therefore well suited for experimental manipulation of status-signaling badges.

## Hypotheses

We tested the following five hypotheses:

1. Badge size is positively correlated to contest success and therefore fighting ability.
2. The lateral stripe is a component of the badge and/or acts as a signal amplifier.
3. More contests initiated by males with reduced badges will result in draws due to signal confusion (an "inferior" signal perceived by the receiver).
4. Rohwer's incongruence hypothesis: enlarged badges are not matched by increased levels of aggression (contest initiation).
5. Badge size is maintained as an honest signal based on independent metabolic costs (i.e., males with larger badges have higher daily energetic costs during the breeding season).

## Methods

### Study Area

We conducted field work during September-October 1996 and 1997 at Augrabies Falls National Park (hereafter Augrabies) (28° 35' S, 20° 20' E), Northern Cape Province, South Africa. Detailed descriptions of the study area can be found in Branch and Whiting (1997) and Whiting and Greeff (1997). Briefly, the most favored habitat at Augrabies are the granitic banks of the Orange River. Granite at Augrabies varies between very smooth and coarse, and lizards use crevices and exfoliating flakes for refuge. The numerous Namaqua fig trees also serve as gathering points. Lizards appear to use these trees for shade and also feed on ripe figs and insects attracted to the trees (Whiting and Greeff 1997, 1999; Greeff and Whiting 2000). Lizards act as dispersal agents for figs (Greeff and Whiting 1999) as well. Rainfall is erratic and occurs during the summer months (<4 to about 39 cm). Augrabies experiences cold winters (as low as -2.90C) and hot summers (as high as 42.9C) (Weather Bureau 1996 in Branch and Whiting 1997).

## Badge-Body Size Relationships

The same individual (MJW) took the following measurements on all males: SVL (nearest mm), head length ( $\pm 0.01$  mm), head width ( $\pm 0.01$  mm), and body mass ( $\pm 0.1$  g). We assumed that any measurement error would be equal for all treatment groups and therefore did not assess measurement error through repeatability of measurements. Prior to release, we uniquely marked each male on the dorsum, using white enamel paint. We quantified the allometric relationship between badge and body size (SVL and mass) by first tracing badge area onto Plexiglas and then onto paper (brand and quality standard for all lizards). Then we cut out and weighed the tracing on a digital balance ( $\pm 0.0001$  g). We traced badges from 383 lizards used in a separate study but from the same location. We also traced badges for males used in the testosterone study. To convert from mass to area ( $\text{MM}^2$ ), we weighed 10 pieces of paper of known area and generated the following equation: badge area =  $0.2015 + 126.82$  (badge mass) ( $r_s = 0.9996$ ,  $F_{1,8} = 19,443.2$ ,  $P < 0.0001$ ). To ensure comparison of dimension-free variables, we cube root transformed mass, square root transformed badge area, and natural log transformed SVL. We also calculated Olsson's (1994a) condition index using the cube root of mass and SVL ( $\text{mass}^{1/3}/\text{SVL}$ ). We investigated allometric relationships using simple linear regression and estimated the relationship between badge area and body size and condition using Pearson correlation coefficients.

## Badge Manipulation

### HYPOTHESES 1 AND 2 (EFFECTS OF BADGE SIZE AND LATERAL STRIPE)

### AND HYPOTHESIS 3 (SMALL BADGE AND SIGNAL CONFUSION)

We manipulated the status-signaling badges of free-ranging males using orange vermilion acrylic paint (Chromacryl®) to increase badge size and black to reduce badge size. Both colors closely resemble natural orange and black on lizards to a human observer. We did not measure spectral properties of badges, and, therefore, the reflectance values of the paint likely did not match that of the badges. This is not ideal and may introduce some bias but should be ameliorated by the controls (discussed next). Further, many lizard taxa have been shown to respond to paint manipulated individuals in what has been perceived as normal behavior (reviewed in Cooper and Greenberg [1992]; Martin and Forsman 1999).

By using orange we controlled for color polymorphism; also, we painted the chest area on all males black (natural color) to control for possible extraneous effects resulting from variable black coloring. We randomly allocated lizards to the following treatments:

1. Control 1: sham painted with a dry brush ( $n = 13$ )
2. Control 2: badge painted with no adjustment to badge size ( $n = 12$ )
3. Badge increased by 30% ( $n = 14$ ; the 30% increase in badge size was visually estimated and may have marginally exceeded natural badge size of the largest individuals)
4. Badge reduced by 30% ( $n = 17$ )
5. Lateral stripe erased ( $n = 24$ )
6. Badge erased ( $n = 19$ )

Of the 119 males we captured and manipulated, 99 (83%) were resighted for behavioural observations. The unpredictability of resighting individual males resulted in differences in sample size among treatment groups.

#### **HYPOTHESIS 4 (ROHWER'S INCONGRUENCE HYPOTHESIS: BADGE SIZE AND AGGRESSION)**

Rohwer's incongruence hypothesis suggests that individuals that do not behave in accordance with the status that their badge conveys will be persecuted by dominants. In Harris' sparrows, only individuals that received an enlarged badge in addition to a testosterone boost rose in social status (Rohwer and Rohwer 1978). We tested whether male aggression in flat lizards was congruent with badge size. We predicted that males with enlarged badges would be more aggressive and therefore initiate more contests. (Contest initiation was used as an index of aggression.) For all contests, we scored which individual was the initiator and quantified the relationship between aggression (contests initiated) and badge size (see Statistical Analyses).

#### **Testosterone Manipulation**

We further explored the relationship between aggression and badge size by manipulating the testosterone levels of free-ranging males. We evaluated the influence of testosterone on aggression and contest success by using two testosterone regimens. The first experimental group of males ( $n = 17$ ) was injected with 600 ng of testosterone (200  $\mu$ l of a 3 mg testosterone/ml saline solution), and the second group ( $n = 16$ ) was similarly injected with 1,000 ng of testosterone (100  $\mu$ l a 10 mg testosterone/ml saline solution). A control group ( $n = 17$ ) was handled similarly and pierced with a syringe needle, but not injected. Released lizards quickly resumed normal behavior, and we collected behavioral data 1.5 or more days after injection, depending on how quickly lizards were resighted in the field.

#### **Costs of Aggression**

##### **HYPOTHESIS 5 (BADGE SIZE AND FIELD METABOLIC RATE)**

**Field Protocol.** We measured field metabolic rates (FMRs) on free-ranging individuals using doubly labeled water (DLW) (Lifson and McClintock 1966; Nagy 1980, 1989). We captured 30 males during morning hours, and each received an intraperitoneal injection of sterile water containing 300 mg of 10 atom percent  $\text{H}_2^{18}\text{O}$  and 2.5 mg of 99.9 atom percent  $^2\text{H}_2\text{O}$ . (DLW-injected males were not used in any other aspect of this study.) We then drew blood from the suborbital sinus using 75  $\mu$ l microhematocrit capillary tubes 2 to 3 h later. We also drew blood from a further four males that were not injected, to be used for measurement of background isotope concentrations. Depending on when they were captured, we released lizards either on the same day, during the late afternoon, or the following morning. Most lizards immediately resumed normal behavior and some males began displaying shortly after release. We flame sealed all blood samples in glass capillary tubes and refrigerated them. We weighed all lizards ( $\pm 0.1$  g), measured them (SVL,  $\pm 1$  mm), and had their badges traced within a few hours of capture. We began recapturing lizards after 9 d, and after 13 d had recaptured 14 of the 30 injected lizards for a second blood sample.

**Laboratory Protocol.** We sent blood samples to the University of California, Los Angeles (UCLA), for isotopic analyses. Blood was distilled under vacuum to obtain pure water, which was analyzed, along with diluted injection solutions, for  $^{18}\text{O}$  concentration by proton activation analysis (at UCLA) (Wood et al. 1975), and for deuterium concentration by gas-isotope-ratio mass spectrometry (at the Boston University isotope laboratory). We estimated body water volumes, necessary for the calculations of FMR, for the times of injection from the dilution volumes of injected oxygen-18 (Nagy 1983). We estimated body water volumes at recapture from body mass, assuming individuals maintained the same fractional body water content during the study. We calculated FMRs using equation 2 in Nagy (1980), as modified from Lifson and McClintock (1966).

We converted rates of CO<sub>2</sub> production to units of energy (joules) using the relationship 25.7 J/ml of CO<sub>2</sub> produced for an insectivorous diet (Nagy 1983).

## Field Observations

We worked in an area in which lizards are habituated to tourists and respond to thrown food. When a marked male was resighted in the field, we altered natural spatial patterns by throwing bread to other nearby males. By reducing neighbor distances, we increased the likelihood of male-male contests between the manipulated male and nearby conspecifics. An independent groups design was employed in which each male was observed once. We recorded the following data for all contests during timed, 10-min trials: (1) initiator, (2) agonistic display (ventral display, ventral display-chase, or chase), and (3) outcome. A ventral display occurs when a male raises the side of his body and flashes his badge at an intruder. Ventral displays may or may not precede a chase and sometimes occur after a short chase. There were no significant (Mann-Whitney tests,  $P > 0.3$ ; two-tailed) differences in contest outcome for ventral displays and ventral display-chases for any treatment group. Therefore, we pooled ventral displays and ventral display-chases for statistical analysis. We determined contest outcomes when one individual left the immediate area in response to agonistic behavior by its rival. If both lizards displayed agonistic behavior and neither individual withdrew, we considered the contest a draw. We timed (seconds) the duration of agonistic interactions only for the testosterone and DLW experiments.

## Statistical Analyses

We assessed differences in body size among treatment groups using the  $\chi^2$  approximation of one-way Kruskal-Wallis analysis of variance (ANOVA) (two-tailed). Males that were not resighted in the field (and therefore lacked behavioral observations) were excluded from this analysis. Contests involving status signaling were analyzed separately from those involving a chase. We made the distinction because a chase always resulted in a win for the initiator and precluded status signaling. We therefore tested for significant differences in contest success as the ratio of ventral display-chase wins to the total number of contests excluding chases. Significant differences among treatment groups in the number of draws were analyzed as the ratio of total draws to the total number of contests excluding chases. Because of the high number of zeros in many of the behavioral categories, we used nonparametric Mann-Whitney tests and Kruskal-Wallis ANOVA for comparison of treatment means. For significant differences, we performed a comparison of mean ranks in which subsets of homogeneous means were grouped together using  $\alpha = 0.05$  (Analytical Software 1996). We assessed behavioral correlations using Spearman rank correlation coefficients. For badge measurements, we established normality using rankit plots and Wilkison-Shapiro tests. We used Spearman rank tests to assess the relationship between badge size and FMR and between FMR and body size (mass). Unless otherwise stated, tests were one-tailed for directional hypotheses. Means are reported  $\pm 1$  SE. All differences were considered significant at  $\alpha < 0.05$ .

## Results

### Badge-Body Size Relationships

Badge area correlated significantly with mass ( $r_s = 0.523$ ,  $n = 379$ ,  $P < 0.0001$ ), SVL ( $r_s = 0.493$ ,  $n = 383$ ,  $P < 0.0001$ ) and body condition ( $\text{mass}^{1/3}/\text{SVL}$ ) ( $r_s = 0.506$ ,  $n = 379$ ,  $P < 0.0001$ ). Badge area scaled allometrically to SVL by the equation: badge area =  $-13.720 + 4.2886 \log_e(\text{SVL})$  ( $F_{1,381} = 122.21$ ,  $P < 0.0001$ ), while it scaled allometrically to body mass by the equation: badge area =  $0.5511 + 2.0179 \log_e(\text{mass})$  ( $F_{1,377} = 142.25$ ,  $P < 0.0001$ ) (Fig. 2-1).

## Badge Manipulation

The treatment groups were not significantly different in SVL ( $H = 5.27$ ,  $P = 0.38$ ), head length ( $H = 5.21$ ,  $P = 0.52$ ), head width ( $H = 5.34$ ,  $P = 0.38$ ), and mass ( $H = 6.66$ ,  $P = 0.25$ ) (Table 2-3).

The behavioral categories for the two control groups showed no significant differences; therefore, the two groups were combined for all statistical comparisons (Mann-Whitney,  $n = 25$ ,  $P > 0.4$  in each case; two-tailed).

### HYPOTHESES 1 AND 2 (EFFECTS OF BADGE SIZE AND LATERAL STRIPE)

Contest success (proportion of ventral display and ventral display chase wins) was significantly different among treatment groups ( $H = 19.03$ ,  $P = 0.0008$ ). Males with enlarged badges won significantly ( $P < 0.05$ ) more contests using ventral displays and ventral display-chases than lizards in the other treatment groups in the order 30% reduction > lateral stripe removed > badge erased. However, contest success between males with enlarged badges and the control group was not significantly different ( $P > 0.05$ ), nor were there differences among the remaining three treatment groups with reduced badges and the control group ( $P > 0.05$ ).

### HYPOTHESIS 3 (SMALL BADGE AND SIGNAL CONFUSION)

The proportion of contests with no outcome (draw) was significantly different among treatment groups ( $H = 11.94$ ,  $P = 0.018$ ), with individuals from reduced badge treatment groups involved in more contests with no outcome (30%, lateral stripe erased) (Table 2-4). However, although an overall treatment effect was detected, the experimentwise error rate was sufficiently high to preclude significant differences ( $P > 0.05$ ) during pairwise comparisons.

### HYPOTHESIS 4 (ROHWER'S INCONGRUENCE HYPOTHESIS: BADGE SIZE AND AGGRESSION)

The mean frequency of all behavior by treatment group is reported in Table 2-4. The total number of contests initiated by all treatment groups was not significantly different ( $H = 6.28$ ,  $P = 0.09$ ), although the number of contests initiated with a ventral display was marginally significant ( $H = 7.88$ ,  $P = 0.05$ ). The number of ventral displays performed was significantly different ( $H = 8.91$ ,  $P = 0.03$ ); males with enlarged badges initiated significantly more contests than males with their badges erased ( $P < 0.05$ ).

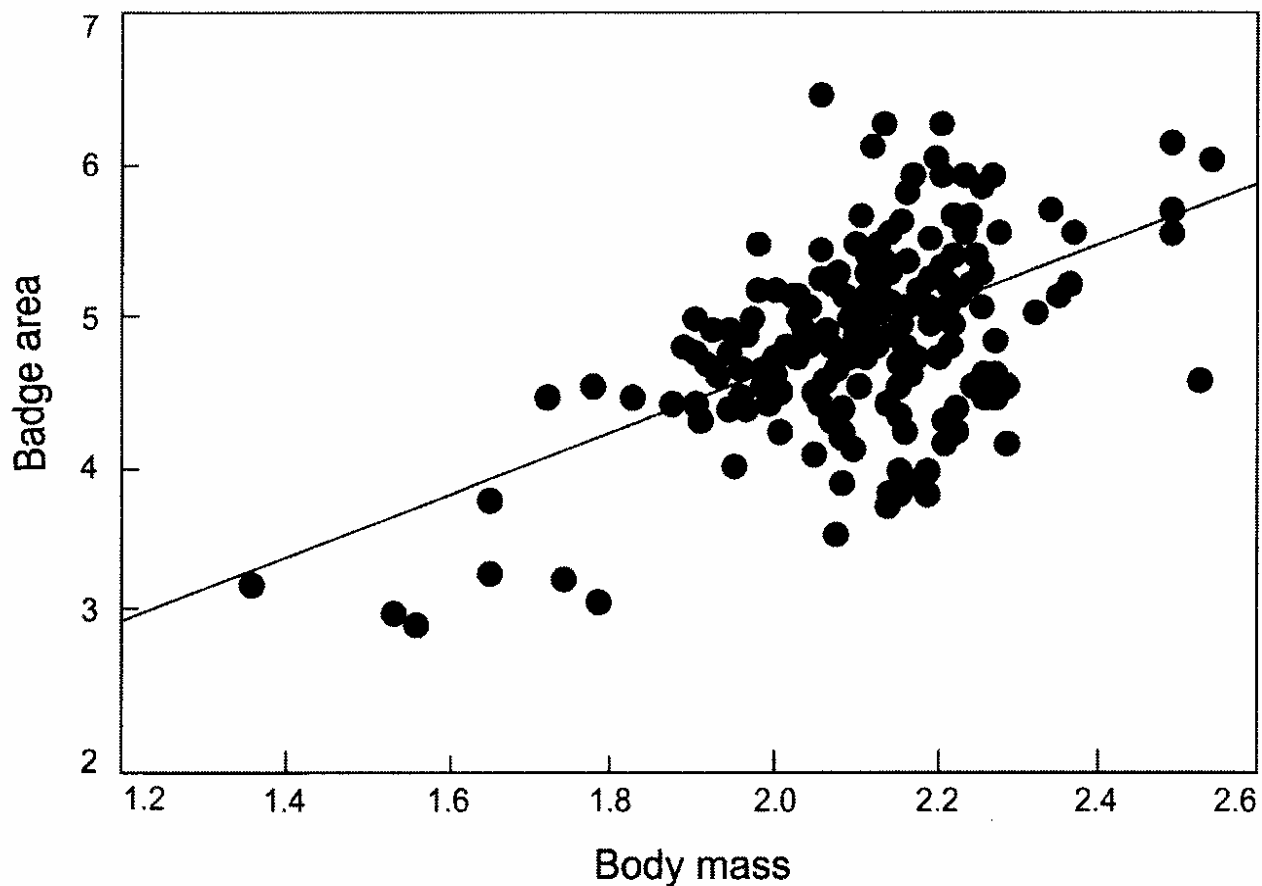
Initiation of contests was significantly correlated with contest outcome (wins) (control group:  $r_s = 0.878$ ,  $P < 0.0001$ ; 30% enlarged:  $r_s = 0.975$ ,  $P < 0.0001$ ; 30% reduced:  $r_s = 0.725$ ,  $P < 0.002$ ; lateral stripe removed:  $r_s = 0.802$ ,  $P < 0.0001$ ; badge erased:  $r_s = 0.97$ ,  $P < 0.0001$ ). A contest sometimes ended in a draw if lizards were equally matched or if the initiator's opponent failed to see the challenger (Table 2-4).

## Manipulation of Testosterone

The two treatment groups and the control were not significantly different in SVL ( $H = 2.275$ ,  $P = 0.321$ ), head length ( $H = 3.284$ ,  $P = 0.194$ ), head width ( $H = 0.331$ ,  $P = 0.847$ ), mass ( $H = 3.785$ ,  $P = 0.151$ ), and badge area ( $H = 0.105$ ,  $P = 0.949$ ) (Table 2-5).

Of the 51 marked lizards, 41 were resighted for behavioral observations (Table 2-5). The number of contests initiated among the three groups was significantly different ( $H = 6.202$ ,  $P = 0.023$ ). Specifically, the second testosterone group initiated significantly more contests than the control group ( $P < 0.05$ ), but neither differed from the first testosterone group ( $P > 0.05$ ) (Table 2-6).





**Figure 2-1** Relationship between badge area (square root transformed) and body mass (cube root transformed). The relationship is given by the equation: badge area = 0.5511 + 2.0179 log<sub>e</sub> (mass).

**Table 2-3** Descriptive statistics of body measurements for six treatment groups. Means are given ± 1 SE. Only lizards for which behavioral interactions were recorded are included (*n* = 99).

	<i>n</i>	SVL (mm)	Head Length (mm)	Head Width (mm)	Mass (g)
Sham painted	13	76.08 ± 0.51	16.45 ± 0.10	13.10 ± 0.09	10.75 ± 0.20
Control painted	12	76.50 ± 0.60	18.92 ± 2.50	13.12 ± 0.16	10.16 ± 0.33
30% Increased	14	76.29 ± 0.67	16.25 ± 0.11	13.00 ± 0.11	10.64 ± 0.22
30% Reduced	17	76.18 ± 0.40	16.22 ± 0.12	13.19 ± 0.13	10.54 ± 0.27
Lateral stripe erased	24	77.17 ± 0.29	16.59 ± 0.10	13.25 ± 0.11	11.04 ± 0.21
Badge erased	19	76.58 ± 0.49	16.33 ± 0.09	13.22 ± 0.11	10.40 ± 0.28

**Table 2-4 Descriptive statistics of behavioral frequencies performed by males with manipulated badges during 10-min observation periods.** Means are given  $\pm$  1 SE. See text and Table 2-3 for treatment group sample sizes.

	Control	30% Enlarged	30% Reduced	Lateral Stripe Removed	Badge Erased
Initiated with ventral display	1.28 $\pm$ 0.26	2.31 $\pm$ 0.49	1.24 $\pm$ 0.47	1.24 $\pm$ 0.24	0.88 $\pm$ 0.33
Total initiated	1.88 $\pm$ 0.40	3.15 $\pm$ 0.71	1.71 $\pm$ 0.53	1.62 $\pm$ 0.30	1.24 $\pm$ 0.40
Ventral display-chase wins	0.88 $\pm$ 0.21	2.31 $\pm$ 0.52	0.35 $\pm$ 0.19	0.33 $\pm$ 0.14	0.29 $\pm$ 0.14
Ventral display-chase: no result	0.44 $\pm$ 0.14	0.15 $\pm$ 0.10	0.76 $\pm$ 0.34	1.00 $\pm$ 0.21	0.47 $\pm$ 0.19
Total ventral displays	1.32 $\pm$ 0.25	2.46 $\pm$ 0.50	1.29 $\pm$ 0.48	1.33 $\pm$ 0.23	0.88 $\pm$ 0.33
Total won	1.52 $\pm$ 0.35	3.08 $\pm$ 0.75	0.76 $\pm$ 0.29	0.71 $\pm$ 0.18	0.88 $\pm$ 0.30

The amount of time engaged in agonistic interactions was significantly different among the three groups ( $H = 7.413$ ,  $P = 0.012$ ). Males in the second testosterone group also spent significantly more time ( $P < 0.05$ ) engaged in agonistic interactions than control males, but neither differed from the first testosterone group ( $P > 0.05$ ) (Table 2-6).

Initiation of contests was significantly positively correlated with contest outcome (wins) (control group:  $r_s = 1.0$ ,  $P < 0.0001$ ; testosterone group 1:  $r_s = 0.926$ ,  $P < 0.0001$ ; testosterone group 2:  $r_s = 0.988$ ,  $P < 0.0001$ ). In a few instances contests resulted in draws ( $n = 2$ ), the opponent ignored the challenge ( $n = 3$ ), or the opponent did not see the challenger ( $n = 5$ ). Contest outcome (wins) was also significantly positively correlated with the amount of time engaged in agonistic interactions (control group:  $r_s = 0.986$ ,  $P < 0.0001$ ; testosterone group 1:  $r_s = 0.858$ ,  $P < 0.0001$ ; testosterone group 2:  $r_s = 0.936$ ,  $P < 0.0001$ ).

## Costs of Aggression

### HYPOTHESIS 5 (BADGE SIZE AND FMR)

Mean measurements for the 14 recaptured lizards relating to FMR are reported in Table 2-7. There was a significant positive correlation between FMR and badge size ( $r_s = 0.31$ ,  $P = 0.03$ ) (Fig. 2-2), but no significant relationship between FMR and body mass ( $r_s = -0.08$ ,  $P > 0.5$ ). We were able to collect limited behavioral data on 12 of the 14 lizards for which FMR was calculated. There was no significant relationship ( $P > 0.5$ ) between aggression (contests initiated/min, type of aggressive behavior, contest duration) and badge size, but this was largely confounded by alternative reproductive strategies (Whiting, unpublished data). The sample split equally into territorial and floater males.

**Table 2-5 Descriptive statistics of body measurements for testosterone and control groups.** Means are given  $\pm$  1 SE. Only lizards for which behavioral interactions were recorded are included ( $n = 41$ ).

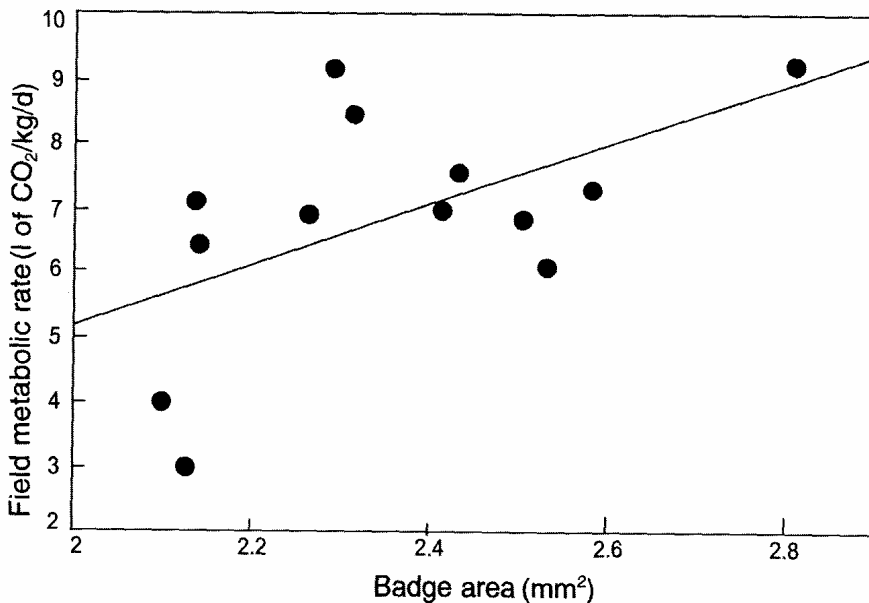
	<i>n</i>	SVL (mm)	Head Length (mm)	Head Width (mm)	Mass (g)	Badge Area (MM2)
Testosterone group 1	14	76.73 $\pm$ 0.46	16.27 $\pm$ 0.11	1122 $\pm$ 0.13	10.59 $\pm$ 0.27	2.76 $\pm$ 0.15
Testosterone group 2	12	77.50 $\pm$ 0.36	16.51 $\pm$ 0.11	13.25 $\pm$ 0.12	11.34 $\pm$ 0.20	2.80 $\pm$ 0.16
Control	15	77.80 $\pm$ 0.59	16.53 $\pm$ 0.13	13.56 $\pm$ 0.30	10.89 $\pm$ 10.26	2.58 $\pm$ 0.22

**Table 2-6 Descriptive statistics of behavioral observations from testosterone experiment (10-min trials).** Means are given  $\pm$  1 SE.

Control ( <i>n</i> = 15)	Testosterone Group 1 ( <i>n</i> = 14)	Testosterone Group 2 ( <i>n</i> = 12)
Contests initiated 1.60 $\pm$ 0.70	3.64 $\pm$ 1.08	4.17 $\pm$ 1.02
Duration of contests (s) 2.27 $\pm$ 1.01	8.86 $\pm$ 3.31	14.08 $\pm$ 6.31
Total contests won 1.60 $\pm$ 0.70	3.21 $\pm$ 1.05	4.00 $\pm$ 0.96

**Table 2-7 Body mass and field metabolic rates (FMRs) of male flat lizards (*n* = 14) in relation to badge size.**

Range	Mean	SE
Body mass (g) 7.90-10.30	9.14	0.19
Measurement period (days) 9.00-15.00	12.20	0.43
Badge area (MM <sup>2</sup> ) 2.10-2.82	2.26	0.05
FMR (l of CO <sub>2</sub> /kg/d) 3.04-9.18	6.91	0.45
FMR (kJ/d) 0.75-2.20	1.61	0.11



**Figure 2-2** Relationship between FMR and badge area. There was a significant ( $P = 0.03$ ) correlation between FMR and badge area (see text). The relationship is given by the equation:  $FMR = -4.0334 + 4.6087 \times \text{badge area}$ .

## DISCUSSION

### Badge Area and Body Condition in Flat Lizards

In an analysis independent of the badge manipulation experiment, body size (mass and SVL) and body condition correlated significantly with badge area. The badge manipulation experiment controlled for differences in body size among treatment groups and thus demonstrated a role for badge area in contest success independently of body size/condition. This suggests that larger and/or older males are therefore superior fighters and badge area is a reliable index of fighting ability. However, the correlation coefficients (range: 0.493-0.523) between body size variables and badge area also show a high degree of scatter. This variation indicates differing abilities of males to settle contests and bear the costs of dominance and suggests that variation in fighting ability is not simply age related. Body condition may be the best indicator of fighting ability because, unlike SVL, which may be more tightly linked to age in an organism with indeterminate growth, body condition could reflect resistance to parasites (Hamilton and Zuk 1982; Moller, Dufva, and Erritzoe 1998) and/or foraging ability (Moller and de Lope 1994), both of which ultimately may affect fitness.

### Badge Area and Contest Success in Flat Lizards

Males with enlarged badges won more contests than other treatment groups. This finding confirms the presence of a status-signaling badge in *P. broadleyi* and demonstrates the importance of badge area in contest success. Status-signaling badges in *P. broadleyi* are polychromatic, which may influence contest success. However, we controlled for color polymorphism by painting the entire badge and chest area using the same paint for all lizards.

Males without a lateral stripe lost significantly more contests than badge-enlarged lizards, but not significantly more than control males, although a trend was apparent. Because lateral stripes are always visible and correlate with ventral badge area, they may passively convey information about the bearer's fighting ability. Further, during signaling, the lateral stripe may function as a signal amplifier (Hasson 1991). The negligible differences among the treatment groups with reduced badges (30% reduction, lateral stripe removed, and badge erased) suggest a threshold below which further badge reduction makes little difference to contest success. Contests resulting in a draw were most frequent among the treatment groups with reduced badges. These lizards were conveying signals that underestimated their fighting ability. This signal confusion may have increased the likelihood of an opponent returning the challenge and resulted in a greater proportion of draws.

### Badge Area and Aggression in Flat Lizards

Males with enlarged badges did not initiate more contests than other treatment groups. However, when this analysis was restricted to contests initiated using a ventral display, the difference was marginally significant. Males with enlarged badges initiated the most contests, and males with their badges erased, the least. Males with enlarged badges also performed significantly more ventral displays than males with their badges erased but did not perform more ventral displays than the other groups. The absence of a strong relationship between contest initiation and badge size among all the treatment groups (excluding enlarged versus erased) could be due to the

ventral placement of the badge. Most males were observed the day following badge manipulation, which may not have been sufficient time for the lizard to become aware of its new phenotype. Olsson (1994a) tested the relationship between badge area and contest success in the lizard *Lacerta agilis*. Although *L. agilis* with enlarged badges initiated more contests, this could be because the lateral placement of badges in *L. agilis* in contrast to the ventrally placed badges in *P. broadleyi* allowed immediate recognition of a manipulated badge. In addition, recognition of this new phenotype is likely to be proximally mediated by testosterone levels. In Harris' sparrows, an increase in badge size failed to influence status because their behavior was incongruent with their new badge size (incongruence hypothesis of Rohwer and Rohwer [1978]). However, males treated with testosterone implants in addition to enlarged badges demonstrated behavior congruent with their new badge size and attained a higher social rank. Male flat lizards with enlarged badges won more contests than males with reduced badges but only initiated more contests after testosterone boosts. This result therefore supports the incongruence hypothesis and highlights the importance of testosterone in agonistic behavior, as has been found for other lizards (e.g., Moore and Lindzey 1992; Tokarz 1995a).

### **Honest Signaling and Maintenance of Signaling Reliability in Flat Lizards**

ESS models suggest that frequency-dependent selection should maintain badges of status as an honest signal, but only if there is a cost independent of fighting (Johnstone and Norris 1993). Badge (or pigment) production was previously thought to be energetically cheap (Kodric-Brown and Brown 1984; Krebs and Dawkins 1984), and this has been shown for melanin production in house finches (*Carpodacus mexicanus*) (Hill and Brawner 1998; but see Veiga and Puerta [1996]). However, carotenoid-based pigments are derived from food and are condition-dependent indicators of quality and are considered costly (Hill and Montgomerie 1994; Olson and Owens 1998). A growing body of literature supports the view that carotenoids are valuable because they are scarce (alternatives are reviewed by Olson and Owens [1998]). Therefore, brightness in males may reflect superior foraging ability and, as a consequence, quality. In general, herbivores ingest more carotenoids than carnivores and omnivores fall somewhere between the two (Olson and Owens 1998). Dietary requirements for birds are obviously very different from lizards (endo- versus ectotherms), especially lizards that are largely carnivorous and have fewer carotenoids available to them. However, *P. broadleyi* do occasionally ingest Namaqua figs and are thus considered omnivorous (Whiting and Greeff 1997). Figs are not readily available and are considered an unpredictable resource (Whiting and Greeff 1997, 1999). Given that *P. broadleyi*'s badge is orange and/or yellow, the role of carotenoids in badge development and expression cannot yet be excluded. However, both the presence and levels of carotenoids in Namaqua figs must first be determined.

Another hypothesis for constraints to cheating is that frequent aggressive encounters mediated through hormones could translate to a higher metabolic rate, providing a proximate cost to badge size (Marler et al. 1995). (In birds, there is also evidence of a three-way interaction among androgen levels, immunocompetence and badge size/dominance [Moller, Kimball, and Eritzoe 1996; Evans, Goldsmith, and Norris 2000; Poiani, Goldsmith, and Evans 2000] [see Table 2-11]). A positive correlation between badge size and metabolic rate has been demonstrated for great tits, pied flycatchers (Roskaft et al. 1986), and willow tits (Hogstad 1987). We found a significant correlation between badge size and FMR, independent of body size. This suggests

that a physiological cost may constrain badge size, such that it honestly signals fighting ability. Unfortunately, we had insufficient data to explore properly the relationship between FMR and levels of aggression (also confounded by males adopting alternative reproductive strategies.)

A further cost of bright coloration is increased risk of predation (e.g., Darwin 1871; Endler 1980; Zuk and Kolluru 1998). Thus, under the handicap principle, ornaments are honest signals because the bearer is able to avoid predation under conditions of increased conspicuousness (either through possessing a larger badge or through behavior such as increased activity that correlates with badge size) (Zahavi 1975, 1977). It is difficult to exclude this possibility in the case of flat lizards; however, their badges are ventrally concealed and in most cases are only briefly exposed during contests.

For a signal to be effective, it must be easily detectable by the receiver in a manner that complements its physical habitat (Fleishman 1988a, 1992; Johnstone 1997). In a rocky landscape devoid of vegetation, individuals of *P. broadleyi* are readily visible. In addition, the orange and/or yellow badge is conspicuous against a black chest. Consequently, their display is simple and devoid of rapid, repeated motion, such as displays used by vegetation-dwelling lizards (e.g., *Anolis auratus*, Fleishman 1988a). In a highly dense population such as at Augrabies, in which male-male contests occur frequently, a readily visible badge of status effectively reduces conflict and risk of injury.

## Future Directions

Of all the work on badges to date, very few studies have dealt with badge ontogeny (see Moller and Erritzoe [1992] and Senar, Copete, and Martin [1998] for birds, and Carpenter [1995b] for lizards). This is a neglected component of badge studies that could shed new light on the influence of badge developmental plasticity on future dominance and, ultimately, on reproductive success. An important issue is whether badges are fixed at birth, or a function of later interactions (continuous). A related issue to this is badge size heritability, for which estimates are reported for great tits (*Parus major*) and house sparrows (*Passer domesticus*) (Pomiankowski and Moller 1995). One way to explore the influence of badge ontogeny is to raise juvenile males in the laboratory under varying social conditions. Some treatment groups could be subjected to controlled interactions in neutral arenas to examine the effects of prior experience on badge development. This would also allow a proper analysis of badge development in relation to body size. The tracing of badges in the field may mask subtle, important differences in badge size. Digital analysis of badge size using pixel counts may be more reliable and should allow fine-grained analysis of variation in badge size in relation to body size and fighting ability. Finally, female mate choice (or preference) could be evaluated in individuals with a known history and in relation to known badge traits (chroma and area).

To develop further theory on the evolution of badges and ritualized encounters between males, more field studies on a variety of taxa are needed. The majority of studies have been on birds, and results of these have sometimes been unequivocal (see Slotow, Alcock, and Rothstein 1993; Senar 1999). In addition, much of the work has focused on the role badges have played in access to food rather than mates. Studies of status signaling in lizards number less than a handful (Table 2-1) but suggest potentially rewarding systems for future work. Compared to birds, many lizards

have polychromatic badges (tree lizards, Zucker [1994a,b] and Carpenter [1995a, b]; flat lizards, this study) and even dual status -signaling badges (Zucker 1994a). Furthermore, unlike most birds (except red-winged blackbirds, Metz and Weatherhead [1992]), flat lizards have concealed badges that are flashed when using distinct behavior, while tree lizards use throat color to signal status. Different selective forces are likely to be at play here.

Unfortunately, there is a poor understanding of what may constrain cheating in lizards. Our study suggests a physiological cost independent of contests. Studies on the relationship between badge size and hormone levels are greatly needed (Whiting and Hews, unpublished data). A recent study by Olsson and Silverin (1997) showed that in sand lizards (*Lacerta agilis*), testosterone plays a trigger function during badge development; phenotypic expression of badge traits (area and chroma) are constrained by resource allocation. The possible link between badge size and resource holding potential (Maynard Smith and Harper 1988), possibly mediated through hormones, requires further investigation. We hope to evaluate more fully badge size and aggression in light of tradeoffs among metabolic rate, androgen levels, and immunocompetence, relative to honest signaling and constraints to cheating. Additionally, the potential role of carotenoids in badge development in lizards with yellow/orange coloration requires investigation. Finally, numerous models now exist showing that deception is likely to occur to some degree (e.g., Johnstone and Grafen 1993; Johnstone and Norris 1993; Semple and McComb 1996). Although many studies have manipulated phenotypes to introduce "cheaters" into a population, almost nothing is known of the incidence of deception in natural populations (but see Adams and Caldwell [1990] and references therein). This is likely to be an extremely challenging line of research but could be key to a better understanding of social evolution.

## **Acknowledgments**

Permission for this work was granted by the National Parks Board of South Africa. The van der Walts, Mombergs, and staff at Augrabies provided logistical support and encouragement. We thank Hayley Komen for painstakingly cutting and weighing badges. MJW is extremely grateful to Debbie Bellars for 2 yr of expert field assistance on several different lizard projects and to Hayley Komen for assistance in 1997. We also thank Francis Thackeray and Bill Cooper for statistical advice. Comments from Troy Baird, Dirk Bauwens, Bill Cooper, Rufus Johnstone, Johnathan Losos, Anders Moller, Mats Olsson, Trevor Richter, and Hannes van Wyk on earlier versions of the manuscript greatly improved its quality. We acknowledge that the reviewers were not always in agreement with our conclusions and acknowledge full responsibility for the viewpoints published here. Juan Carlos Senar and some of the reviewers listed above kindly provided reprints and key references. Graham Alexander provided advice and equipment for the DLW component of the study; Duncan Mitchell and Helen Laburn did the same and generously provided the deuterium at no charge (all University of the Witwatersrand). Robert Michener (Boston University) measured deuterium in samples. MJW thanks Stanley Fox, Troy Baird, and Kelly McCoy for inviting him to take part in the symposium and for generous financial assistance via the National Science Foundation and the Herpetologists' League. Financial assistance from Hannes van Wyk (University of Stellenbosch) and the Department of Biology at the University of California at Los Angeles made the DLW study possible and is especially appreciated. Additional support was provided to MJW by the National Research Foundation, South Africa.





**Plate 1** Male *Platysaurus broadleyi*. Males are polymorphic for front leg color, which may be yellow, orange, or an orange-yellow mixture. Photograph by M.J. Whiting.



**Plate 2** Ventral view of a male *Platysaurus broadleyi* showing abdominal status signalling-badge (light-color). Badges may be orange, yellow, or an orange-yellow mixture. Photograph by M.J. Whiting.



**Plate 3** Male *Platysaurus broadleyi* flashing his badge at a rival (termed a ventral display). Males also simultaneously expand their throats. Photograph by M.J. Whiting.



**Plate 4** Status signalling can break down during competition for high-quality resources and result in fighting, which is preceded by back arching and lunging. Photograph by M.J. Whiting.

## References

- Adams, E.S., and R.L. Caldwell. 1990. Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Anim. Behav.* 39:706-716.
- Adams, E.S., and M. Mesterson-Gibbons. 1995. The cost of threat displays and the stability of deceptive communication. *J. theor. Biol.* 175:405-421.
- Analytical Software. 1996. *Statistix for windows*. Analytical Software, Tallahassee, Florida.
- Andersson, M.A. 1994. *Sexual selection*. Princeton University Press, Princeton, New Jersey.
- Andersson, M.A., and Y. Iwasa. 1996. Sexual selection. *TREE* 11:53-58.
- Arak, A. 1983. Sexual selection by male-male competition in natterjack toad choruses. *Nature* 306:261-262.
- Arak, A., and M. Enquist. 1993. Hidden preferences and the evolution of signals. *Phil. Trans. R. Soc. Lond. B* 340:207-213.
- Balphy, M.H., D.F. Balphy, and H.C. Romesburg. 1979. Social status signaling in winter flocking birds: an examination of a current hypothesis. *Auk* 96:78-93.
- Barlow, G.W., W. Rogers, and N. Fraley. 1986. Do Midas cichlids win through prowess or daring? It depends. *Behav. Ecol. Sociobiol.* 19:1-8.
- Beani, L., and S. Turillazzi. 1999. Stripes display in hover-wasps (Vespidae: Stenogastrinae): a socially costly status badge. *Anim. Behav.* 57:1233-1239.
- Belthoff, J.R., A.M. Dufty, Jr., and S.A. Gauthreaux, Jr. 1994. Plumage variation, plasma steroids and social dominance in male house finches. *Condor* 96:614-625.
- Berglund, A., A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* 58:385-399.
- Branch, W.R., and M.J. Whiting. 1997. A new *Platysaurus* (Squamata: Cordylidae) from the Northern Cape Province, South Africa. *African J. Herpetol.* 46:124-136.
- Brooks, R., and V. Couldridge. 1999. Multiple sexual ornaments coevolve with multiple mating preferences. *Am. Nat.* 154:37-45.
- Bryant, D.M., and A.V. Newton. 1994. Metabolic cost of dominance in dippers, *Cinclus cinclus*. *Anim. Behav.* 48:447-455.
- Carpenter, G.C. 1995a. The ontogeny of a variable social badge: throat color development in tree lizards (*Urosaurus ornatus*). *J. Herpetol.* 29:7-13.
- . 1995b. Modeling dominance: the influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetol. Monogr.* 9:88-101.
- Chappell, M.A., M. Zuk, T.H. Kwan, and T.S. Johnsen. 1995. Energy cost of an avian vocal display: crowing in red jungle fowl. *Anim. Behav.* 49:255-257.
- Clutton-Brock, T.H. and S.D. Albon. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145-170.
- Collis, K., and G. Borgia. 1992. Age-related effects of testosterone, plumage, and experience on aggression and social dominance in juvenile male satin bowerbirds (*Ptilonorhynchus violaceus*). *Auk* 109:422-434.
- Cooper, W.E., Jr., and L.J. Vitt. 1987. Deferred agonistic behavior in a long-lived scincid lizard *Eumeces laticeps*: Field and laboratory data on the roles of body size and residence in agonistic strategy. *Oecologia* 72:321-326.
- Cooper, W.E., Jr., and N. Greenberg. 1992. Reptilian coloration and behavior. In *Biology of the Reptilia. Vol. 18. Brain, hormones, and behavior*, edited by C. Gans and D. Crews, 298-422. University of Chicago, Chicago.

- Darwin, C. 1871. *The descent of man, and selection in relation to sex*. The Modern Library, New York.
- Davies, N.B. and T.R. Halliday. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* 274:683-685.
- Dawkins, M.S. 1993. Are there general principles of signal design? *Phil. Trans. R. Soc. Lond. B* 340:251-255.
- Dawkins, M.S., and T. Guilford. 1991. The corruption of honest signalling. *Anim. Behav.* 41:865-873.
- Dawkins, R., and J.R. Krebs. 1978. Animal signals: information or manipulation? In *Behavioural ecology: an evolutionary approach*, edited by J.R. Krebs and N.B. Davies, 1<sup>st</sup> edition, 282-309. Blackwell Scientific Publications, Oxford.
- de Boer, B.A. 1980. A causal analysis of the territorial and courtship behaviour of *Chromis cyanea* (Pomacentridae, Pisces). *Behaviour* 73:1-50.
- Endler, J.A. 1980. Natural selection on colour patterns in *Poecilia reticulata*. *Evolution* 34:76-91.
- . 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.* 139:S125-S153.
- . 1993. Some general comments on the evolution and design of animal communication systems. *Phil. Trans. R. Soc. Lond. B* 340:215-225.
- Endler, J.A., and A.E. Houde. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* 49:456-468.
- Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Anim. Behav.* 33:1152-1161.
- Enquist, M., and O. Leimar. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. theor. Biol.* 102:387-410.
- Enquist, M., O. Leimar, T. Ljungberg, Y. Mallner, and N. Segerdahl. 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Anim. Behav.* 40:1-14.
- Evans, M.R. 1991. The size of adornments of male scarlet-tufted malachite sunbirds varies with environmental conditions, as predicted by handicap theories. *Anim. Behav.* 42:797-803.
- Evans, M.R., and K. Norris. 1996. The importance of carotenoids in signaling during aggressive interactions between male firemouth cichlids (*Cichlasoma meeki*). *Behav. Ecol.* 7:1-6.
- Evans, M.R., A.R. Goldsmith, and S.R.A. Norris. 2000. The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behav. Ecol. Sociobiol.* 47:156-163.
- Fleishman, L.J. 1986. Motion detection in the presence and absence of background motion in an *Anolis* lizard. *J. Comp. Physiol. A, Sensory, Neural Behav. Physiol.* 159:711-720.
- . 1988a. Sensory and environmental influences on display form in *Anolis auratus*, a grass anole from Panama. *Behav. Ecol. Sociobiol.* 22:309-316.
- . 1988b. The social behavior of *Anolis auratus*, a grass anole from Panama. *J. Herpetol.* 22:13-23.
- . 1988c. Sensory influences on physical design of a visual display. *Anim. Behav.* 36:1420-1424.
- . 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Amer. Nat.* 139:S36-S61.

- Folstad, I., and A.J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* 139:603-622.
- Fox, S.F., N.A. Heger, and L.S. Delay. 1990. Social cost of tail loss in *Uta stansburiana*: lizard tails as status-signalling badges. *Animal. Behav.* 39:549-554.
- Furlow, B., R.T. Kimball, and M.C. Marshall. 1998. Are rooster crows honest signals of fighting ability? *Auk* 115:763-766.
- Getty, T. 1998. Handicap signalling: when fecundity and viability do not add up. *Anim. Behav.* 56:127-130.
- Godfray, H.C.J. 1995. Signalling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am. Nat.* 146:1-24.
- Gonzalez, G., G. Sorci, and F. de Lope. 1999a. Seasonal variation in the relationship between cellular immune response and badge size in male house sparrows (*Passer domesticus*). *Behav. Ecol. Sociobiol.* 46:117-122.
- Gonzalez, G., G. Sorci, A.P. Møller, P. Ninni, C. Haussy, and F. de Lope. 1999b. Immunocompetence and condition-dependent sexual advertisement in male house sparrows (*Passer domesticus*). *J. Anim. Ecol.* 68:1225-1234.
- Grafen, A. 1990. Biological signals as handicaps. *J. theor. Biol.* 144:517-546.
- Grafen, A., and R.A. Johnstone. 1993. Why we need ESS signalling theory. *Phil. Trans. R. Soc. Lond. B* 340:245-250.
- Greeff, J.M., and M.J. Whiting. 1999. Dispersal of Namaqua fig seeds by the lizard *Platysaurus broadleyi* (Sauria: Cordylidae). *J. Herpetol.* 33:328-330.
- Greeff, J.M., and M.J. Whiting. 2000. Foraging-mode plasticity in the lizard *Platysaurus broadleyi*. *Herpetologica*. In press.
- Greenfield, M.D. 1997. Sexual selection and the evolution of advertisement signals. In *Perspectives in ethology, volume 12*, edited by D.H. Owings, M.D. Beecher and N.S. Thompson, 145-177. Plenum Press, New York.
- Greenfield, M.D., and R.L. Minckley. 1993. Acoustic dueling in tarbush grasshoppers: Settlement of territorial contests via alternation of reliable signals. *Ethology* 95:309-326.
- Guilford, T., and M.S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. *Anim. Behav.* 42:1-14.
- . 1995. What are conventional signals? *Anim. Behav.* 49:1689-1695.
- Halperin, J.R.P., T. Giri, J. Elliott, and, D.W. Dunham. 1998. Consequences of hyper-aggressiveness in Siamese fighting fish: cheaters seldom prospered. *Anim. Behav.* 55:87-96.
- Hamilton, W.D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384-387.
- Hasson, O. 1991. Sexual displays as amplifiers: practical examples with an emphasis on feather decorations. *Behav. Ecol.* 2:189-197.
- Hill, G.E., and W.R. Brawner, III. 1998. Melanin-based plumage coloration in the house finch is unaffected by coccidial infection. *Proc. R. Soc. Lond. B* 265:1105-1109.
- Hill, G.E., and R. Montgomerie. 1994. Plumage colour signals nutritional condition in the house finch. *Proc. R. Soc. Lond. B* 258:47-52.
- Hogstad, O. 1987. It is expensive to be dominant. *Auk* 104:333-336.
- Holberton, R.L., K.P. Able, and J.C. Wingfield. 1989. Status signalling in dark-eyed juncos, *Junco hyemalis*: plumage manipulations and hormonal correlates of dominance. *Anim. Behav.* 37: 681-689.

- Horn, A.G., M.L. Leonard, and D.M. Weary. 1995. Oxygen consumption during crowing by roosters: talk is cheap. *Anim. Behav.* 50:1171-1175.
- Huhta, E., and R.V. Alatalo. 1993. Plumage colour and male-male interactions in the pied flycatcher. *Anim. Behav.* 45:511-518.
- Hurd, P.L. 1997a. Is signalling of fighting ability costlier for weaker individuals? *J. theor. Biol.* 184:83-88.
- . 1997b. Cooperative signalling between opponents in fish fights. *Anim. Behav.* 54:1309-1315.
- Iwasa, Y., A. Pomiankowski, and S. Nee. The evolution of costly mate preferences II. The “handicap” principle. *Evolution* 45:1431-1442.
- Järvi, T., and M. Bakken. 1984. The function of the variation in the breast stripe of the great tit (*Parus major*). *Anim. Behav.* 32:590-596.
- Järvi, T., Ø. Walsø, and M. Bakken. 1987. Status signalling by *Parus major*: an experiment in deception. *Ethology* 76:334-342.
- Johnstone, R.A. 1995a. Honest advertisement of multiple qualities using multiple signals. *J. theor. Biol.* 177:87-94.
- . 1995b. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol. Rev.* 70:1-65.
- . 1996. Multiple displays in animal communication: ‘backup signals’ and ‘multiple messages’. *Phil. Trans. R. Soc. Lond. B* 351:329-338.
- . 1997. The evolution of animal signals. Pp. 155-178, in J.R. Krebs and N.B. Davies (eds.), *Behavioural ecology: an evolutionary approach*, 4th ed. Blackwell Scientific Publications, Oxford.
- Johnstone, R.A., and A. Grafen. 1993. Dishonesty and the handicap principle. *Anim. Behav.* 46:759-64.
- Johnstone, R.A., and K. Norris. 1993. Badges of status and the cost of aggression. *Behav. Ecol. Sociobiol.* 32:127-134.
- Jones, I.L. 1990. Plumage variability functions for status signalling in least auklets. *Anim. Behav.* 39:967-975.
- Keys, G.C. and S.I. Rothstein, 1991. Benefits and cost of dominance and subordination in white-crowned sparrows and the paradox of status signalling. *Anim. Behav.* 42:899-912.
- Kim, Y.-G. 1995. Status signalling games in animal contests. *J. theor. Biol.* 176:221-231.
- Kodric-Brown, A., and J.H. Brown. 1984. Truth in advertising: the kinds of traits favoured by sexual selection. *Amer. Nat.* 124:309-323.
- Krakauer, D.C. and M. Pagel. 1995. Spatial structure and the evolution of honest cost-free signalling. *Proc. R. Soc. Lond. B* 260:365-372.
- Krebs, J.R., and R. Dawkins. 1984. Animal signals: mind reading and manipulation. Pp. 380-402 in J.R. Krebs and N.B. Davies, eds. *Behavioural ecology. An evolutionary approach*. Blackwell Scientific Publications, Oxford.
- Krebs, J.R., and N.B. Davies. 1993. *An introduction to behavioural ecology*, 3rd ed. Blackwell Scientific Publications, Oxford.
- Leal, M. 1999. Honest signalling during prey-predator interactions in the lizard *Anolis cristatellus*. *Anim. Behav.* 58:521-526.
- Leal, M., and J.A. Rodríguez-Robles. 1997. Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Anim. Behav.* 54:1147-1154.

- Leonard, M.L. and A.G. Horn. 1995. Crowing in relation to status in roosters. *Anim. Behav.* 49:1283-1290.
- Lifson, N., and R. McClintock. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *J. theor. Biol.* 12:46-74.
- Marler, C.A., G. Walsberg, M.L. White, and M. Moore. 1995. Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. *Behav. Ecol. Sociobiol.* 37:225-231.
- Martín, J., and A. Forsman. 1999. Social costs and development of nuptial coloration in male *Psammmodromus algirus* lizards: an experiment. *Behav. Ecol.* 10:396-400.
- Mateos, C. and J. Carranza. 1997. The role of bright plumage in male-male interactions in the ring-necked pheasant. *Anim. Behav.* 54:1205-1214.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge, Cambridge University Press.
- . 1991. Honest signalling: the Philip Sydney game. *Anim. Behav.* 42:1034-1035.
- . 1994. Must reliable signals always be costly? *Anim. Behav.* 47:1115-1120.
- Maynard Smith, J., and D.G. Harper. 1988. The evolution of aggression: can selection generate variability? *Phil. Trans. R. Soc. Lond. B* 319:557-570.
- . 1995. Animal signals: models and terminology. *J. theor. Biol.* 177:305-311.
- Maynard Smith, J., and G.A. Parker. 1976. The logic of asymmetric contests. *Anim. Behav.* 24:159-175.
- McGregor, P.K. 1993. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Phil. Trans. R. Soc. Lond. B* 340:237-244.
- . 1995. Animal signals: models and terminology. *J. theor. Biol.* 177:305-311.
- Metz, K.J., and P.J. Weatherhead. 1992. Seeing red: uncovering coverable badges in red-winged blackbirds. *Anim. Behav.* 43:223-229.
- Møller, A.P. 1987a. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Anim. Behav.* 35:1637-1644.
- . 1987b. Social control of deception among status signalling house sparrows *Passer domesticus*. *Behav. Ecol. Sociobiol.* 20:307-311.
- . 1988. Badge size in the house sparrow *Passer domesticus*: Effects of intra- and intersexual selection. *Behav. Ecol. Sociobiol.* 22:373-378.
- Møller, A.P., and de Lope, F. 1994. Differential costs of a secondary sexual character: an experimental test of the handicap principle. *Evolution* 48:1676-1683.
- Møller, A.P., and J. Erritzøe. 1992. Acquisition of breeding coloration depends on badge size in male house sparrows *Passer domesticus*. *Behav. Ecol. Sociobiol.* 31:271-277.
- Møller, A.P., and A. Pomiankowski. 1993. Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.* 32:167-176.
- Møller, A.P., R.T. Kimball, and J. Erritzøe. 1996. Sexual ornamentation, condition, and immune defence in the house sparrow *Passer domesticus*. *Behav. Ecol. Sociobiol.* 39:317-322.
- Møller, A.P., R. Dufva, and J. Erritzøe. 1998. Host immune function and sexual selection in birds. *J. Evol. Biol.* 11:703-719.
- Moore, M.C., and J. Lindzey. 1992. The physiological basis of sexual behavior in male reptiles. Pp. 70-113 in C. Gans and D. Crews (eds.), *Biology of the Reptilia*, Vol. 18. Univ. Chicago Press, Chicago, Illinois.
- Morris, M.R., and M.J. Ryan. 1996. Sexual differences in signal-receiver coevolution. *Anim. Behav.* 52:1017-1024.

- Morris, M.R., M. Mussel, and M.J. Ryan. 1995. Vertical bars on male *Xiphophorus multilineatus*: a signal that deters rival males and attracts females. *Behav. Ecol.* 6:274-279.
- Nagy, K.A. 1980. CO<sub>2</sub> production in animals: analysis of potential errors in the doubly labeled water method. *Amer. J. Physiol.* 238:R466-R473.
- . 1983. *The doubly labeled water (<sup>3</sup>HH<sup>18</sup>O) method: a guide to its use*. University of California, Los Angeles Publication 12-1417:1-45. University of California, Los Angeles.
- . 1989. Doubly labeled water studies of vertebrate physiological ecology. In *Stable isotopes in ecological research*, edited by P.W. Rundel, J.R. Ehleringer, and K.A. Nagy, 270-287. Springer Verlag, New York.
- Olson, V.A., and I.P.F. Owens. Costly sexual signals: are carotenoids rare, risky or required? *TREE* 13:510-514.
- Olsson, M. 1992. Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. *Anim. Behav.* 44:386-388.
- . 1993a. Nuptial coloration and predation risk in model sand lizards, *Lacerta agilis*. *Anim. Behav.* 46:410-412.
- . 1993b. Contest success and mate guarding in male sand lizards, *Lacerta agilis*. *Anim. Behav.* 46:408-409.
- . 1994a. Nuptial colouration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. *Anim. Behav.* 48:607-613.
- . 1994b. Why are sand lizard males (*Lacerta agilis*) not equally green? *Behav. Ecol. Sociobiol.* 35:169-173.
- Olsson, M., and B. Silverin. 1997. Effects of growth rate on variation in breeding coloration in male sand lizards (*Lacerta agilis*: Sauria). *Copeia* 1997:456-460.
- Owens, I.P.F., and I.R. Hartley. 1991. "Trojan sparrows": evolutionary consequences of dishonest invasion for the badges-of-status model. *Am. Nat.* 138:1187-1205.
- Poiani, A., A.R. Goldsmith, and M.R. Evans. 2000. Ectoparasites of house sparrows (*Passer domesticus*): an experimental test of the immunocompetence handicap hypothesis and a new model. *Behav. Ecol. Sociobiol.* 47:230-242.
- Pomiankowski, A. 1987. Sexual selection: the handicap principle does work—sometimes. *Proc. R. Soc. Lond. B* 231:123-145.
- Pomiankowski, A., and A.P. Møller. 1995. A resolution of the lek paradox. *Proc. R. Soc. Lond. B* 260:21-29.
- Qvarnström, A. 1997. Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proc. R. Soc. Lond. B* 264:1225-1231.
- Qvarnström, A., and E. Forsgren. 1998. Should females prefer dominant males? *TREE* 13:498-501.
- Reyer, H.-U., W. Fischer, P. Steck, T. Nabulon, and P. Kessler. 1998. Sex-specific nest defense in house sparrows (*Passer domesticus*) varies with badge size of males. *Behav. Ecol. Sociobiol.* 42:93-99.
- Rohwer, S. 1975. The social significance of avian winter plumage variability. *Evolution* 29:593-610.
- . 1977. Status signalling in Harris sparrows: some experiments in deception. *Behaviour* 61:107-129.



- . 1982. The evolution of reliable and unreliable badges of fighting ability. *Amer. Zool.* 22:531-546.
- Rohwer, S., and F.C. Rohwer. 1978. Status signalling in Harris sparrows: experimental deceptions achieved. *Anim. Behav.* 26:1012-1022.
- Rohwer, S., and P.W. Ewald. 1981. The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* 35:441-454.
- Roper, T. 1986. Badges of status in avian societies. *New Scient.* 6 February:38-40.
- Røskaft, E., T. Järvi, M. Bakken, C. Bech, R.E. Reinertsen. 1986. The relationship between social status and resting metabolic rate in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). *Anim. Behav.* 34:838-842.
- Ryan, M.J., and A.S. Rand. 1993. Sexual selection and signal evolution: the ghost of biases past. *Phil. Trans. R. Soc. Lond. B* 340:187-195.
- . 1995. Female responses to ancestral advertisement calls in Túngara frogs. *Science* 269:390-392.
- Ryan, M.J., J.H. Fox, W. Wilczynski, and A.S. Rand. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* 343:66-67.
- Salvador, A., J.P. Veiga, J. Martín, and P. López. 1997. Testosterone supplementation in subordinate, small male lizards: consequences for aggressiveness, color development, and parasite load. *Behav. Ecol.* 8:135-139.
- Semple, S., and K. McComb. 1996. Behavioural deception. *TREE* 11:434-437.
- Senar, J.C. 1999. Plumage colouration as a signal of social status. In *Proceedings of the 22<sup>nd</sup> international ornithological congress, Durban*, edited by N.J. Adams and R.H. Slotow, 1669-1686. BirdLife South Africa, Johannesburg.
- Senar, J.C., and M. Camerino. 1998. Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). *Proc. R. Soc. Lond. B* 265:1515-1520.
- Senar, J.C., M. Camerino, J.L. Copete, and N.B. Metcalfe. 1993. Variation in black bib of the Eurasian siskin (*Carduelis spinus*) and its role as a reliable badge of dominance. *Auk* 110:924-927.
- Senar, J.C., J.L. Copete, and A.J. Martin. 1998. Behavioural and morphological correlates of variation in the extent of postjuvenile moult in the siskin *Carduelis spinus*. *IBIS* 140:661-669.
- Senar, J.C., V. Polo, F. Uribe, and M. Camerino. 2000. Status signalling, metabolic rate and body mass in the siskin: the cost of being a subordinate. *Anim. Behav.* 59:103-110.
- Shields, W.M. 1977. The social significance of avian winter plumage variability: a comment. *Evolution* 31:905-907.
- Slagsvold, T., S. Dale, and A. Kruszewicz. 1995. Predation favours cryptic coloration in breeding male pied flycatchers. *Anim. Behav.* 50:1109-1121.
- Slotow, R., J. Alcock, and S.I. Rothstein. 1993. Social status signalling in white-crowned sparrows: an experimental test of the social control hypothesis. *Anim. Behav.* 46:977-989.
- Solberg, E.J., and T.H. Ringsby. 1997. Does male badge size signal status in small island populations of house sparrows, *Passer domesticus*? *Ethology* 103:177-186.
- Studd, M.V., and R.J. Robertson. 1985a. Evidence for reliable badges of status in territorial yellow warblers (*Dendroica petechia*). *Anim. Behav.* 33:1102-1113.
- Studd, M.V., and R.J. Robertson. 1985b. Sexual selection and variation in reproductive strategy in male yellow warblers (*Dendroica petechia*). *Behav. Ecol. Sociobiol.* 17:101-109.

- Számadó, S. 2000. Cheating as a mixed strategy in a simple model of aggressive communication. *Anim. Behav.* 59:221-230.
- Thompson, C.W., and M.C. Moore. 1991. Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. *Anim. Behav.* 42:745-753.
- Tokarz, R.R. 1995. Importance of androgens in male territorial acquisition in the lizard *Anolis sagrei*: an experimental test. *Anim. Behav.* 49:661-669.
- Tuttle, M.D., and M.J. Ryan, 1981. Bat predation and the evolution of vocalisations in the neotropics. *Science* 214:677-8.
- Veiga, J.P. 1993. Badge size, phenotypic quality, and reproductive success in the house sparrow: a study of honest advertisement. *Evolution* 47:1161-1170.
- . 1995. Honest signaling and the survival cost of badges in the house sparrow. *Evolution* 49:570-572.
- Veiga, J.P., and M. Puerta. 1996. Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proc. R. Soc. Lond. B* 263:229-234.
- Viljugrein, H. 1997. The cost of dishonesty. *Proc. R. Soc. Lond. B* 264:815-821.
- Whitfield, D.P. 1986. Plumage variability and territoriality in breeding turnstone *Arenaria interpres*: status signalling or individual recognition? *Anim. Behav.* 34:1471-1482.
- . 1987. Plumage variability, status signalling and individual recognition in avian flocks. *TREE* 2:1318.
- . 1988. The social significance of plumage variability in wintering turnstone *Arenaria interpres*. *Anim. Behav.* 36:408-415.
- Whiting, M.J. 1999. When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. *Behav. Ecol. and Sociobiol.* 46:210-214.
- Whiting, M.J., and J.M. Greeff. 1997. Facultative frugivory in the Cape flat lizard, *Platysaurus capensis* (Sauria: Cordylidae). *Copeia* 1997:811-818.
- . 1999. Use of heterospecific cues by the lizard *Platysaurus broadleyi* for food location. *Behav. Ecol. and Sociobiol.* 45:420-423.
- Whiting, M.J., and P.W. Bateman. 1999. Male preference for large females in the lizard *Platysaurus broadleyi* (Sauria: Cordylidae). *J. Herpetol.* 33:309-312.
- Wickler, W. 1957. vergleichende verhaltenstudien an grundfischen. I. Bertra ge zür biologie, besonders zur ethologie von *Blenius fluviatilis* asso im vergleich zu einigen anderen bodenfischen. *Z. Tierpsychol.* 14:393-428.
- Wilson, J.D. 1992. A re-assessment of the significance of status signalling in populations of wild great tits, *Parus major*. *Anim. Behav.* 43:999-1009.
- Wood, R.A., K.A. Nagy, N.S. MacDonald, S.T. Wakakuwa, R.J. Beckman, and H. Kaaz. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. *Analyt. Chem.* 47:646-650.
- Zahavi, A. 1975. Mate selection – a selection for a handicap. *J. theor. Biol.* 53:205-214.
- . 1977. The cost of honesty (further remarks on the handicap principle). *J. theor. Biol.* 67:603-605.
- Zimmerer, E.J., and K.D. Kallman. 1988. The inheritance of vertical barring (aggression and appeasement signals) in the pygmy swordtail, *Xiphophorus nigrensis* (Poeciliidae, Teleostei). *Copeia* 1988:299-307.
- Zucker, N. 1994a. A dual status-signalling system: a matter of redundancy or differing roles? *Anim. Behav.* 47:15-22.

- . 1994b. Social influence on the use of a modifiable status signal. *Anim. Behav.* 48:1317-1324.
- Zuk, M., T.S. Johnsen, and T. Maclarty. 1995. Endocrine-immune interactions, ornaments and mate choice in red jungle fowl. *Proc. R. Soc. Lond. B* 260:205-210.
- Zuk, M., and G.R. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. *Quart. Rev. Biol.* 73:415-438.