

A performance-based cost to honest signalling in male green anole lizards (*Anolis carolinensis*)

Simon P. Lailvaux*, Rebecca L. Gilbert and Jessica R. Edwards

Department of Biological Sciences, The University of New Orleans, 2000 Lakeshore Drive,
New Orleans, LA 70148, USA

Sexual signals are considered costly to produce and maintain under the handicap paradigm, and the reliability of signals is in turn thought to be maintained by these costs. Although previous studies have investigated the costly nature of signal production, few have considered whether honesty might be maintained not by the costliness of the signal itself, but by the costs involved in producing the signalled trait. If such a trait is itself costly to produce, then the burden of energetic investment may fall disproportionately on that trait, in addition to any costs of signal maintenance that may also be operating. Under limited resource conditions, these costs may therefore be great enough to disrupt an otherwise reliable signal-to-trait relationship. We present experimental evidence showing that dietary restriction decouples the otherwise honest relationship between a signal (dewlap size) and a whole-organism performance trait (bite force) in young adult male *Anolis carolinensis* lizards. Specifically, while investment in dewlap size is sustained under low-resource condition relative to the high-resource treatment, investment in bite force is substantially lower. Disruption of the otherwise honest dewlap size to bite force relationship is therefore driven by costs associated with the expression of performance rather than the costs of signal production in *A. carolinensis*.

Keywords: whole-organism performance; life-history; diet; honest signalling

1. INTRODUCTION

Male weapons and secondary sexual signals that are used during male combat have been linked to a variety of traits that increase the likelihood of victory during fights with rival males in several animal species [1]. However, in order for receivers to be able to glean information about traits related to fighting ability from signal expression, signals must be reliable or honest indicators of those traits [2,3]. Under classical honest signalling and ‘handicap’ models, the reliability and honesty of animal signals are thought to be maintained by the costs of signal expression and/or maintenance (reviewed in [3]). Male advertisement and threat signals, for example, are typically viewed as handicaps such that only select males are able to bear the costs of intensive signalling ([4–6], but see [7,8] for an opposing view). Indeed, signals may impose a variety of costs on the bearer (reviewed in [9]), which may maintain the overall reliability of a signalling system because they prevent individuals from signalling a higher level of fighting ability than they actually possess.

Whereas the link between costly signals and signalled traits has been well explored, it is typically only the costs of the signal itself that are thought to be important for maintaining signal reliability. The costs involved in expressing the signalled trait, by contrast, are seldom considered. Because male secondary sexual signals are often linked to physiological traits that are themselves costly to produce and maintain [10], it is plausible that the maintenance or developmental costs of trait expression,

in addition to the various costs of signalling, could affect the overall signal-to-trait relationship. For example, male weapons and signals used during male–male combat are typically linked to a variety of functional and behavioural traits that together comprise an individual’s fighting ability or resource-holding potential. Recent studies have focused especially on whole-organism performance abilities (i.e. any measure of an organism conducting a dynamic, ecologically relevant task such as jumping, running or biting, as defined in earlier studies [11,12]) as important determinants of male combat outcomes [13–15]. Specific performance traits are not only key predictors of the likelihood of victory in escalated, physical combat, but are also often positively correlated, independent of body size, with sexual signal expression in several taxa, including some beetles and lizards (reviewed in [12]). Because performance capacities are themselves supported by a variety of physiological and metabolic pathways that need to be sustained during escalated male combat [16–19], they may impose significant developmental and maintenance costs on the bearer. These physiological costs of performance and combat may in turn have consequences for the development and maintenance of reliable signals if they are expensive enough to draw limited energetic resources away from signal expression.

Although unreliable or deceptive signals are considered rare and/or difficult to detect, a handful of studies have demonstrated the existence of dishonest signals in natural populations. For example, the regenerated male claws of several species of male fiddler crabs are dishonest signals of fighting ability, which in these animals hinges partly on

* Author for correspondence (slailvaux@gmail.com).

the whole-organism performance abilities of endurance and claw closing force [20–22]. In a recent study using the crayfish *Cherax dispar*, Wilson *et al.* [23] showed that male crayfish invest more in producing large claws than they do in producing high-quality claw muscle, resulting in claws that are weaker than might be expected based on claw size alone. Thus, the unreliable nature of the male signal in this species appears for the most part to depend not on the costs of signal production or maintenance, but on the cost of high-quality muscle production. Indeed, muscle is relatively costly to produce [24] and operate [25,26], and muscle production has been shown to trade-off against other important fitness-related phenotypes, such as fecundity [27] and testes size [28] in a variety of invertebrate species. Given these and other life-history trade-offs with physiological traits [26], costs of performance may potentially constrain or otherwise impinge on honest signal production.

Identification of fitness-related traits whose maintenance and expression are prioritized through allocation of acquired energetic resources has been a primary goal of life-history studies [29]. Although much attention has been paid to allocation, acquisition is at least as important given that limitation of resources is an ubiquitous feature of natural environments [30]. A useful technique is therefore to limit the amount of resources available for acquisition, thereby exposing and magnifying any allocation trade-offs that might be present. Studies of this type have been conducted on a variety of behavioural, morphological and physiological characters [26,31], but the potential resource-mediated links between whole-organism performance traits and secondary sexual signals have received relatively little attention. Performance is integrated within a complex phenotype [32], and as such the expression of performance may both affect and be affected by relative investment in other fitness-enhancing tasks, including those linked to reproduction [26,33]. If performance traits are linked to secondary sexual signals in a condition-dependent manner (i.e. through differential allocation of the pool of acquired resources; see [34]), then manipulation of resource availability may disrupt that link if either the performance trait or the signal is prioritized for continued energetic investment under low-resource conditions.

The green anole, *Anolis carolinensis*, is an ideal vertebrate species for examining life-history trade-offs in performance signalling. Adult *A. carolinensis* males possess a striking secondary sexual character: a large dewlap that is used in a variety of ecological contexts, including encounters with predators [35], displays towards females [36,37], male–male combat [38] and undirected territorial displays [39]. Moreover, the male dewlap is an honest signal of a whole-organism performance capacity (i.e. bite force) in young adult male *A. carolinensis*, as well as in a variety of other territorial anole species [40,41]. Specifically, the overall area of the extended dewlap is significantly positively correlated (independent of body size) with maximum bite force in young adult males [42], suggesting that rivals may glean information on an individual's bite force from the size of his dewlap, most probably in the initial stages of interactions over long ranges [37,43]. Indeed, bite force has previously been shown to predict male combat outcomes in those sexually dimorphic anole species that appear to

use dewlap size to signal bite force (such as *A. carolinensis*; [15]) but not in less-dimorphic species where no link between dewlap size and bite force exists [41]. Importantly, there is no direct mechanistic relationship between dewlap display and bite force, as different muscles are responsible for each (i.e. the ceratohyoid and jaw adductor muscles for dewlap extension and biting, respectively). Dewlaps are therefore 'conventional signals' as defined by Searcy & Nowicki [3].

We conducted a simple dietary restriction experiment using wild-caught *A. carolinensis* juvenile males to test the effect of reduced resource availability on the development of bite force and dewlap size over ontogeny, as well as on the relationship between them. We predicted that limiting the amount of resources available for acquisition would hamper the development and expression of bite force in male lizards raised to sexual maturity, given the putative developmental costs of producing the robust heads and jaw adductor muscles necessary for generating high male bite forces [44]. By contrast, we posit that dewlap development would not suffer a decrement given that the *relative* costs of dewlap development in terms of size are likely to be much less. This is because dewlaps comprise little more than pigmented skin supported by a thin ceratobranchial cartilage, which is in turn extended by relatively small ceratohyoid muscles on each side of the throat [45]. Finally, we predicted that, as a result of these differential costs to bite force and dewlap expression, the relationship between bite force and dewlap size would be decoupled in restricted animals when the lizards reach sexual maturity.

2. METHODS

All procedures, including dietary restriction, were approved by the University of New Orleans Institutional Animal Care Committee (IACUC protocol no. UNO-09-004). Animals were monitored closely for signs of distress or sickness. Restricted diet individuals were placed on an ad libitum diet following the end of the experiment and ate normally when offered food.

(a) Lizard housing and diet treatment

We collected 27 juvenile male *A. carolinensis* lizards (<47 mm snout–vent length (SVL)) from a single natural population in Orleans parish, New Orleans, LA in April 2010 and brought them back to the laboratory at the University of New Orleans. Lizards were housed individually in 30 × 16 × 16 cm cages lined with cypress mulch and identical 30 × 0.5 cm perches oriented towards uniform 75 W light bulbs positioned at the same location over each cage, providing ample opportunity for basking. All cages were located in a constant temperature (25°C) room set to a 12 L:12 D photoperiod to minimize external environmental influences during development. We covered the sides of each cage with dark paper to prevent the lizards seeing each other. We allocated lizards randomly to one of two diet treatments: an unrestricted diet treatment where lizards were provided with crickets ad libitum ($n = 13$) and a restricted diet where lizards were given one similar-sized cricket three times per week ($n = 14$). Crickets were dusted with ample Fluker's Repta vitamin powder (Fluker Farms, Louisiana) to ensure that all lizards received adequate vitamins and minerals regardless of diet treatment. Lizards were kept in the laboratory under

these conditions and feeding regimes for three months, which is sufficient time for juvenile green anoles to attain sexual maturity. The relationship between dewlap size and bite force is age-dependent in *A. carolinensis* males such that the dewlaps of much older and larger males (specifically 'heavyweight' males >64 mm SVL; see [15]) do not honestly signal bite force [42]. We therefore only considered young 'lightweight' adult males in the current study, both because of the time required for lizards to attain heavyweight status (approx. 2–3 years in nature; S. P. Lailvaux 2009, unpublished data), and because heavyweight males are less common than lightweights in natural *A. carolinensis* populations [15,46].

(b) Measurement of morphology, dewlap size and bite force

For each lizard, we measured the following variables once every four weeks: mass, SVL (measured from the tip of the lizard's snout to the cloaca), dewlap area and bite force. To measure dewlap area, we positioned the lizard sideways along a countertop and used forceps to gently pull the ceratobranchial forward near the articulation with the basihyoid, thereby fully extending the dewlap. We photographed extended dewlaps against a 1 × 1 cm grid using a Canon A610 Powershot digital camera mounted on a tripod, and digitized the resulting images using tpsDig v. 1.3.1. This method has previously been shown to yield repeatable results in a variety of *Anolis* lizard species, including *A. carolinensis* [41,42,47]. We measured *in vivo* bite force using an isometric Kistler force transducer (type 9023, Kistler, Winterthur, Switzerland) connected to a type 5058a Kistler charge amplifier (see [48,49] for a detailed description) using standard methods. Briefly, we induced lizards to bite down by placing the free ends of the plates between their jaws. Lizards were placed in an incubator set to 32°C (similar to field body temperatures for this species in New Orleans; [50]) for 1 h prior to bite force measurement and between trials. Bite force was measured five times per individual, and the largest value from the five trials was considered to be the maximum bite force for that individual ([51]; for discussion of the use of maximum values in performance studies, see [52]).

(c) Analyses

We compared starting values for SVL, body mass, dewlap size and bite force using two-tailed *t*-tests. To test for differences in growth curves between the restricted and unrestricted diet treatments for SVL and mass, we used a general linear mixed-model with diet treatment as a fixed factor and individual as a random factor (to account for repeated measures) fit by restricted estimated maximum likelihood (REML) and implemented using the *lme* function of the *nlme* package (S. P. Lailvaux 2010, unpublished data) for R (R Core Development Team 2010). Because functional traits such as bite force typically scale positively with body size in a variety of animal taxa, including *A. carolinensis* [15,53], it is necessary to control for size effects in studies of this type. To compare the growth curves for dewlap size and bite force independent of body size, we included SVL as a covariate in these mixed models. To assess the relationship between dewlap size and bite force independent of body size in young adult males, we included both dewlap area and SVL as predictor variables in a multiple regression on bite force. The resulting partial regression coefficients express the relationships between dewlap size and bite force, with body size effects statistically removed [54]. This approach

is analogous to residual analysis but has the advantage of not losing a degree of freedom ([43,55]; see [21,56] for examples). Separate multiple regressions were conducted for the restricted and unrestricted diet treatments. (Note, however, that the size-free relationships between bite force and dewlap size are illustrated using residuals derived from regressions of dewlap size versus SVL and bite force versus SVL, consistent with previous studies; see [21,41] for similar examples.)

3. RESULTS

The two randomly assigned diet treatment groups did not differ in SVL ($n = 27$, d.f. = 2, $t = -0.589$, $p > 0.561$), mass ($n = 27$, d.f. = 2, $t = -0.21$, $p > 0.84$), bite force ($n = 27$, d.f. = 2, $t = -0.3$, $p > 0.77$) or dewlap size ($n = 27$, d.f. = 2, $t = 0.499$, $p > 0.622$) at the start of the experiment. The general linear mixed-models for SVL (figure 1a) and mass (figure 1b) showed that the growth curves for both measures of size differed significantly between the two diet treatments (significant interaction between diet and time; table 1). The growth curves for bite force also differed significantly between restricted and unrestricted diets (figure 1c), independent of body size (significant time × diet interaction; table 1). However, the growth curves for dewlap size (figure 1d) were not significantly different either between the two diet treatments alone, or in conjunction with time (table 1). Examination of the relationship between dewlap size and bite force independent of SVL for the (now-young adult) males in the final measurement period from the two diet treatments showed that a significant relationship was consequently maintained in the individuals placed on the unrestricted diet (table 2a and figure 2a), consistent with the relation observed for males of similar age in the field [42], whereas no significant relationship exists within the restricted diet individuals (table 2b and figure 2b). (Note that diagnostic plots indicated no outliers based on examination of Cook's distances for either model. Model-fitting including a quadratic term also showed no evidence for nonlinear relationships between dewlap size and bite force in individuals on either restricted or non-restricted diets.) Thus, low-diet individuals appear to prioritize investment in dewlap size relative to bite force, such that bite force and dewlap size are effectively decoupled in the restricted diet individuals.

4. DISCUSSION

Under classical Zahavi–Grafen handicap theoretical models, signal reliability is thought to be maintained by the various costs of signalling. However, if signals are linked to traits that are themselves relatively costly to produce, then reliability may be limited by those costs rather than, or in addition to, costs associated with the signal. We tested several predictions relating to relative investment in dewlap size and bite force under limited resource availability in young adult *A. carolinensis*. Males raised on restricted diets attained significantly smaller SVL (figure 1a) and mass (figure 1b) by the end of the study when compared with males raised on ad libitum diets. Thus, dietary restriction significantly affected overall growth, resulting in smaller and lighter adult lizards than the unrestricted treatment. Even taking into account the effect of

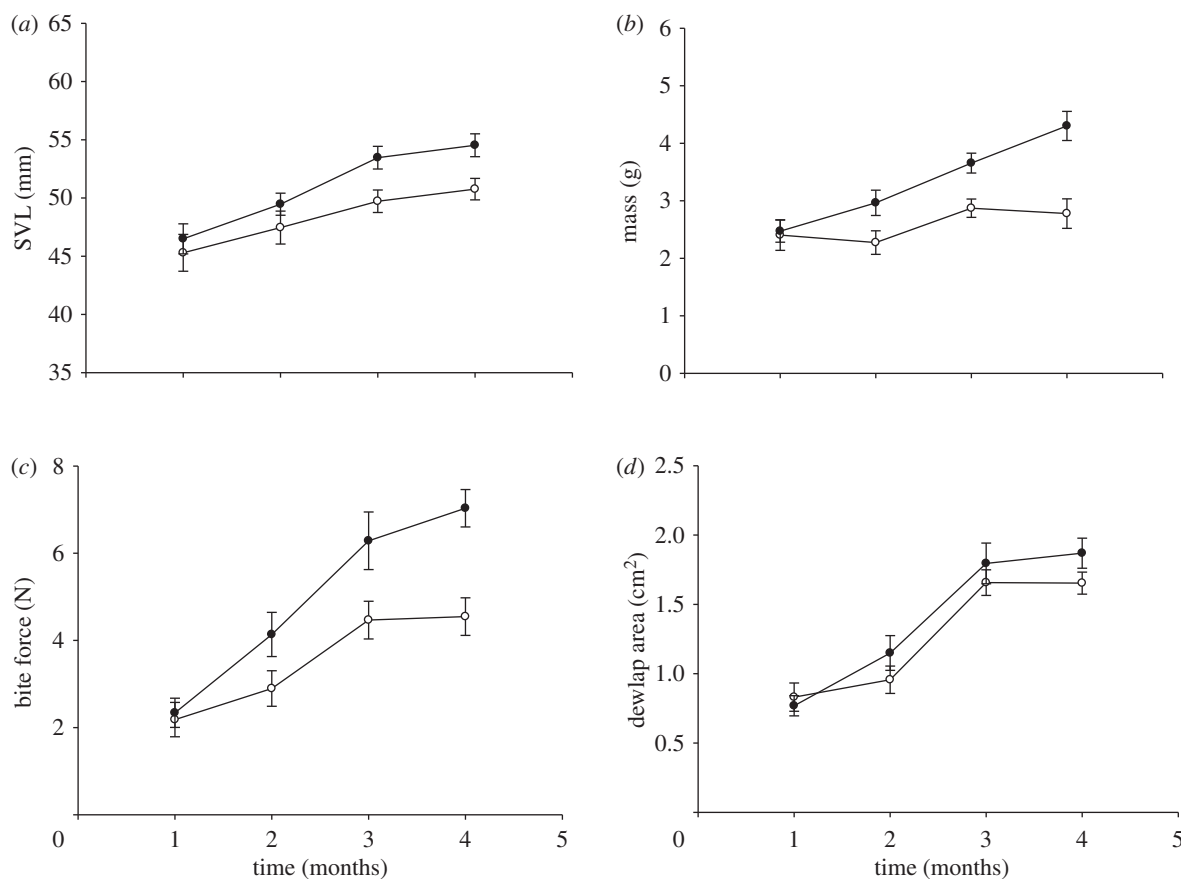


Figure 1. Effects of restricted (open circles) and unrestricted diets (closed circles) on (a) SVL, (b) mass, (c) bite force and (d) dewlap size in male *A. carolinensis*. Error bars represent ± 1 s.e.

Table 1. Results of the general linear mixed models describing growth in SVL, mass, bite force and dewlap size in *A. carolinensis* males raised on restricted and unrestricted diets over three months. Significant values are in bold.

traits	d.f.	<i>F</i>	<i>p</i> -value	traits	d.f.	<i>F</i>	<i>p</i> -value
SVL				mass			
time	3.73	47.71	<0.001	time	3.73	35.8	<0.001
diet	1.25	0.52	0.4790	diet	1.25	0.05	0.8241
time \times diet	3.73	3.63	0.017	time \times diet	3.73	11.19	<0.001
bite force				dewlap			
time	3.72	17.34	<0.001	time	3.70	17.53	<0.001
diet	1.25	0.04	0.848	diet	1.25	1.181	0.288
SVL	1.72	37.8	<0.001	SVL	1.70	37.73	<0.001
time \times diet	3.72	6.35	<0.001	time \times diet	3.70	1.45	0.235

restriction on size, restricted individuals exhibited significantly lower growth in bite force than those on unrestricted diets (figure 1c) but showed no difference in dewlap development from the unrestricted group (figure 1d), in both cases consistent with our predictions. The striking consequence of this differential growth of bite force and dewlap size in restricted individuals is that the significant and positive correlation between bite force and dewlap size that is seen in young adult males of this species in nature [42], and that is also seen in the unrestricted diet treatment in the current study (figure 2a), is absent in the restricted treatment group (figure 2a). Dewlaps that are typically an honest signal of bite force in *A. carolinensis* and other territorial anole species [41,57] are thus rendered unreliable under

limiting resource conditions owing to differential allocation of resources in bite force and dewlap development. This result suggests that the costly nature of performance, and of other traits like performance that are linked to signal expression, might have important implications for the maintenance of reliable signalling in nature.

(a) Costs of performance

The costly and condition-dependent nature of whole-organism performance has received little attention in the context of animal signalling, and placing these findings within a comparative context is therefore problematic. However, similar costs to performance expression have

Table 2. (a) Results of a multiple regression with dewlap size and snout-vent length (SVL) as predictors and bite force as the dependent variable for males raised on the unrestricted diet. Adjusted r^2 is 0.604. (b) Results of a multiple regression with the same variables for males raised on the restricted diet. Adjusted r^2 is 0.495. Significant values are in bold.

	variable	coefficient	s.e.	T	p -value
(a) unrestricted males					
bite force (N)	intercept	-8.81	4.55		
	SVL	0.281	0.09	2.52	0.033
	dewlap size	2.12	0.78	2.71	0.024
(b) restricted males					
bite force (N)	intercept	-12.6	4.91		
	SVL	0.341	0.11	3.072	0.013
	dewlap size	-0.03	1.28	-0.023	0.98

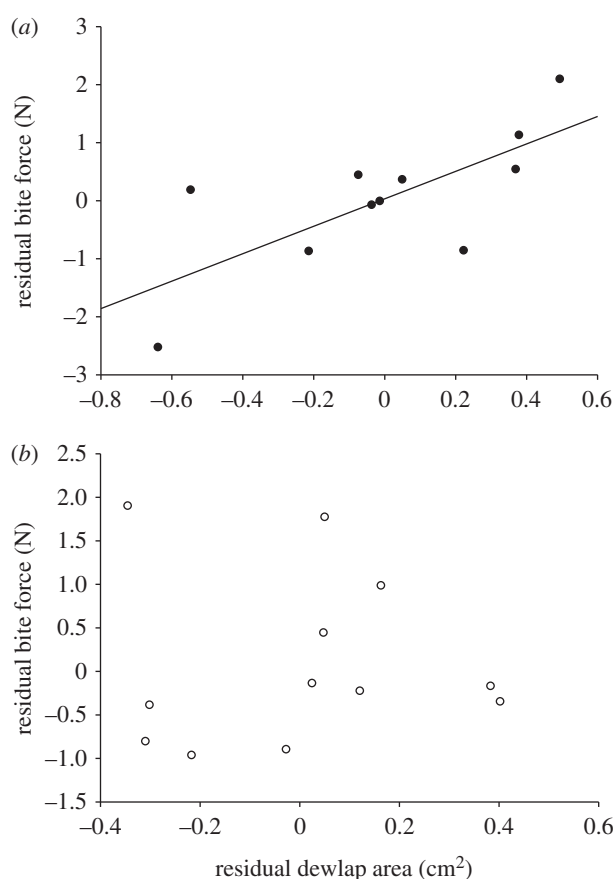


Figure 2. Relationship between residual (i.e. SVL corrected) dewlap area and bite force for (a) unrestricted and (b) restricted diets.

been noted in several other taxa. For example, pull-resisting strength (i.e. the ability to resist being pulled out of tunnels, an important determinant of fighting ability in some dung beetles), which is linked to horn size independent of body size in the beetle *Euoniticellus intermedius* [56], is strongly affected by resource availability in fighting male *Onthophagus taurus* beetles [58]. Similarly, *Xiphophorus helleri* fish that are subject to juvenile dietary restriction show a reduced capacity to increase swimming endurance through training later in life when compared with fish on ad libitum diets ([59], but see [60] who showed that fast-start swimming performance is unaffected by diet treatment in this species). Thus, performance traits appear to be generally costly, such that investment in performance cannot be maintained under low-resource

conditions. The handful of studies where performance costs have been considered within the context of signalling systems are also not directly comparable with our results; for example, in the case of the condition-dependent abdomen drumming rate in wolf spiders [61], the performance trait and the signal are one and the same. A similar honest signalling system involving performance was also studied by Brandt [6], who showed that endurance performance is limited by the expression of a signal (a laterally compressed threat display that probably inhibits respiration and circulation) in the lizard *Uta stansburiana*. However, the causality in these two systems is different, in that dewlap size and bite force in *A. carolinensis* are linked developmentally rather than mechanically. Future studies examining the links between sexual signals and physiological traits would be valuable for understanding the costs of such relationships, as well as any potential modifying factors.

(b) Costs of dishonesty

If high bite forces are more costly to develop than large dewlaps, then what keeps the relationship between bite force and dewlap size honest in young lightweight adult males, as is seen in natural *A. carolinensis* populations [42,57]? Indeed, the apparently low production costs of dewlaps relative to bite force suggest that males may be able to bluff rivals by simply growing large dewlaps without the concomitant development of large jaw adductor muscles, analogous to the large claws and low-quality muscle in *C. dispar* crayfish [23]. (Consistent with the notion that it is the jaw adductor muscles specifically whose growth is compromised, the restricted diet-treatment lizards exhibit significantly narrower heads than the unrestricted treatment animals; S. P. Lailvaux 2010, unpublished data.) One potential reason for individuals in nature to maintain high bite force instead of bluffing is that bite force in lizards is important in several ecological contexts besides male combat, including feeding [48,62] and anti-predator behaviour [63–65]. Thus, while allocating resources away from bite force development may allow males to bluff rivals during the early stages of competitive interactions where bite force is important (cf. [21,23]), it may also result in decrease in fitness in other selective contexts (but see [66]). The fitness costs to expressing a poor bite force in terms of total selection (see [67,68] for discussion) might therefore outweigh the energetic costs of bite force development. Since our results show that bite force does not appear to be ‘protected’ from resource allocation in this way, a more

likely possibility is that honesty may be maintained in nature via receiver-dependent costs if deceptive signallers are exposed through escalated combat with 'honest' individuals (cf. [21]). The costs of such escalated combat can be substantial in *A. carolinensis*, resulting in severe injury or even death [15,69], and hence may be an important factor limiting the evolution of dishonesty in this system. This scenario is consistent with recent theoretical models suggesting that it is the cost of cheating that maintains signal honesty, rather than any inherent cost to the signal itself (reviewed in [8]).

Although the costs of dewlap production are relatively low, honesty could also be maintained by high receiver-independent costs of dewlap display. Just as bite force may be important to more than just male combat, dewlaps are thought to have several different signalling functions in a variety of intra- and interspecific ecological contexts in *Anolis* [70,71]. If displaying in any or all of these contexts incurs fitness costs through, for example, increased likelihood of predation, then dewlap size might possibly be constrained by receiver-independent costs, regardless of the cost of bite force expression. Indeed, studies of visual signalling in particular suggest that dewlaps play an important role in general anole ecology in contexts besides sexual selection [72,73]. Furthermore, Irschick *et al.* [47] showed that individual male dewlaps decrease in size in both the field and the laboratory following the cessation of major breeding activity in a New Orleans *A. carolinensis* population, suggesting that there may indeed be some cost to bearing large dewlaps. Additional data on the role of the dewlap in the life history of *A. carolinensis* are required in order to understand both the fitness value and costs of dewlap expression in this species, and thus to properly target the costs that affect signal reliability in this species.

5. CONCLUSIONS

Identifying and quantifying the many potential costs to signal production and maintenance remain significant challenges to evolutionary ecology. Here, we present evidence for a performance-based cost to honest signalling in a model vertebrate species. Although the condition-dependence of sexual signals is well known, similar condition-dependence of signalled traits—in this case, bite force—is seldom considered. Given that whole-organism capacities such as bite force are particularly costly to develop and maintain owing to the inherently expensive nature of muscle production and maintenance, these results are likely to be relevant to other systems in which energetically costly traits are linked to signal production. These findings highlight the necessity of determining the type and nature of traits that are signalled in animal communication and not just the signals themselves.

Thanks to M. Veronica Lopez for assistance with lizard maintenance. This paper was greatly improved by comments from J. Henningsen, R. Knell and two anonymous reviewers.

REFERENCES

- Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
- Maynard-Smith, J. & Harper, D. 2004 *Animal signals*. Oxford, UK: Oxford University Press.
- Searcy, W. A. & Nowicki, S. (eds) 2005 *The evolution of animal communication: reliability and deception in signaling systems*. Monographs in behavior and ecology. Princeton, NJ: Princeton University Press.
- Grafen, A. 1990 Biological signals as handicaps. *J. Theor. Biol.* **144**, 517–546. (doi:10.1016/S0022-5193(05)80088-8)
- Zahavi, A. 1975 Mate selection: a selection for a handicap. *J. Theor. Biol.* **53**, 205–214. (doi:10.1016/0022-5193(75)90111-3)
- Brandt, Y. 2003 Lizard threat display handicaps endurance. *Proc. R. Soc. Lond. B* **270**, 1061–1068. (doi:10.1098/rspb.2003.2343)
- Getty, T. 2006 Sexually selected signals are not similar to sports handicaps. *Trends Ecol. Evol.* **21**, 83–88. (doi:10.1016/j.tree.2005.10.016)
- Számádó, S. 2011 The cost of honesty and the fallacy of the handicap principle. *Anim. Behav.* **81**, 3–10. (doi:10.1016/j.anbehav.2010.08.022)
- Kotiaho, J. S. 2001 Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biol. Rev.* **76**, 365–376. (doi:10.1017/S1464793101005711)
- Badyaev, A. V. 2004 Developmental perspective on the evolution of sexual ornaments. *Evol. Ecol. Res.* **6**, 975–991.
- Bennett, A. F. & Huey, R. B. 1990 Studying the evolution of physiological performance. In *Oxford surveys in evolutionary biology* (eds D. J. Futuyma & J. Antonovics), pp. 251–284. Oxford, UK: Oxford University Press.
- Lailvaux, S. P. & Irschick, D. J. 2006 A functional perspective on sexual selection: insights and future prospects. *Anim. Behav.* **72**, 263–273. (doi:10.1016/j.anbehav.2006.02.003)
- Hall, M. D., McLaren, L., Brooks, R. C. & Lailvaux, S. P. 2010 Interactions among performance capacities predict male combat outcomes in the field cricket *Teleogryllus commodus*. *Funct. Ecol.* **24**, 159–164. (doi:10.1111/j.1365-2435.2009.01611.x)
- Mowles, S. L., Cotton, P. A. & Briffa, M. 2010 Whole-organism performance capacity predicts resource-holding potential in the hermit crab *Pagurus bernhardus*. *Anim. Behav.* **80**, 277–282. (doi:10.1016/j.anbehav.2010.05.004)
- Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J. & Irschick, D. J. 2004 Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proc. R. Soc. Lond. B* **271**, 2501–2508. (doi:10.1098/rspb.2004.2891)
- Bennett, A. F. 1991 The evolution of activity capacity. *J. Exp. Biol.* **160**, 1–23.
- Garland, T. J. 1984 Physiological correlates of locomotory performance in a lizard: an allometric approach. *Am. J. Physiol.* **247**, R806–R815.
- Jayne, B. C., Bennett, A. F. & Lauder, G. V. 1990 Muscle recruitment during terrestrial locomotion: how speed and temperature affect fibre type use in a lizard. *J. Exp. Biol.* **152**, 101–128.
- Thorpe, K. E., Taylor, A. C. & Huntingford, F. A. 1995 How costly is fighting? Physiological effects of sustained exercise and fighting in swimming crabs, *Necora puber* (L.) (Brachyura, Portunidae). *Anim. Behav.* **50**, 1657–1666. (doi:10.1016/0003-3472(95)80019-0)
- McLain, D. K., McBrayer, L. D., Pratt, A. E. & Moore, S. 2010 Performance capacity of fiddler crab males with regenerated versus original claws and success by claw type in territorial contests. *Ethol. Ecol. Evol.* **22**, 37–49. (doi:10.1080/03949370903515950)
- Lailvaux, S. P., Reaney, L. T. & Backwell, P. R. Y. 2009 Dishonest signalling of fighting ability and multiple performance traits in the fiddler crab *Uca mjoebergi*. *Funct.*

- Ecol.* **23**, 359–366. (doi:10.1111/j.1365-2435.2008.01501.x)
- 22 Backwell, P. R. Y., Christy, J. H., Telford, S. R., Jennions, M. D. & Passmore, N. I. 2000 Dishonest signalling in a fiddler crab. *Proc. R. Soc. Lond. B* **267**, 719–724. (doi:10.1098/rspb.2000.1062)
- 23 Wilson, R. S., Angilletta Jr., M. J., James, R. S., Navas, C. & Seebacher, F. 2007 Dishonest signals of strength in male slender crayfish (*Cherax dispar*) during agonistic encounters. *Am. Nat.* **170**, 284–291. (doi:10.1086/519399)
- 24 Marden, J. H. 1989 Bodybuilding dragonflies: costs and benefits of maximizing flight muscle. *Physiol. Zool.* **62**, 505–521.
- 25 Marden, J. H., Fitzhugh, G. H. & Wolf, M. R. 1998 From molecules to mating success: integrative biology of muscle maturation in a dragonfly. *Am. Zool.* **38**, 528–544.
- 26 Zera, A. J. & Harshman, L. G. 2001 The physiology of life-history trade-offs in animals. *Ann. Rev. Ecol. Syst.* **32**, 95–126. (doi:10.1146/annurev.ecolsys.32.081501.114006)
- 27 Marden, J. H. 2000 Variability in the size, composition, and function of insect flight muscles. *Ann. Rev. Physiol.* **62**, 157–178. (doi:10.1146/annurev.physiol.62.1.157)
- 28 Saglam, I. K., Roff, D. A. & Fairbairn, D. J. 2008 Male sand crickets trade-off flight capability for reproductive potential. *J. Evol. Biol.* **21**, 997–1004. (doi:10.1111/j.1420-9101.2008.01548.x)
- 29 Stearns, S. C. 1989 Trade-offs in life-history evolution. *Funct. Ecol.* **3**, 259–268. (doi:10.2307/2389364)
- 30 Kokko, H. 1998 Good genes, old age and life-history trade-offs. *Evol. Ecol.* **12**, 739–750. (doi:10.1023/A:1006541701002)
- 31 Roff, D. A. 1992 *The evolution of life histories*. New York, NY: Chapman & Hall.
- 32 Ghalambor, C. K., Walker, J. A. & Reznick, D. N. 2003 Multi-trait selection, adaptation, and constraints on the evolution of burst swimming performance. *Integr. Comp. Biol.* **43**, 431–438. (doi:10.1093/icb/43.3.431)
- 33 Ghalambor, C. K., Reznick, D. N. & Walker, J. A. 2004 Constraints on adaptive evolution: the functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *Am. Nat.* **164**, 38–50. (doi:10.1086/421412)
- 34 Tomkins, J. L., Radwan, J., Kotiaho, J. S. & Tregenza, T. 2004 Genic capture and resolving the lek paradox. *Trends Ecol. Evol.* **19**, 323–328. (doi:10.1016/j.tree.2004.03.029)
- 35 Leal, M. 1999 Honest signalling during predator–prey interactions in the lizard *Anolis cristatellus*. *Anim. Behav.* **58**, 521–526. (doi:10.1006/anbe.1999.1181)
- 36 Sigmund, W. R. 1983 Female preference for *Anolis carolinensis* males as a function of dewlap color and background coloration. *J. Herpetol.* **17**, 137–143. (doi:10.2307/1563454)
- 37 Orrell, K. S. & Jenssen, T. A. 2003 Heterosexual signalling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. *Behaviour* **140**, 603–634. (doi:10.1163/156853903322149469)
- 38 Jenssen, T. A., Decourcy, K. R. & Congdon, J. D. 2005 Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters? *Anim. Behav.* **69**, 1325–1336. (doi:10.1016/j.anbehav.2004.07.023)
- 39 Decourcy, K. R. & Jenssen, T. A. 1994 Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Anim. Behav.* **47**, 251–262. (doi:10.1006/anbe.1994.1037)
- 40 Vanhooydonck, B., Herrel, A. Y., Van Damme, R. & Irschick, D. J. 2005 Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Funct. Ecol.* **19**, 38–42. (doi:10.1111/j.0269-8463.2005.00940.x)
- 41 Lailvaux, S. P. & Irschick, D. J. 2007 The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *Am. Nat.* **170**, 573–586. (doi:10.1086/521234)
- 42 Vanhooydonck, B., Herrel, A., Van Damme, R., Jay Meyers, J. & Irschick, D. J. 2005 The relationship between dewlap size and performance changes with age and sex in a green anole (*Anolis carolinensis*) lizard population. *Behav. Ecol. Sociobiol.* **59**, 157–165. (doi:10.1007/s00265-005-0022-y)
- 43 Darlington, R. B. & Smulders, T. V. 2001 Problems with residual analysis. *Anim. Behav.* **62**, 599–602. (doi:10.1006/anbe.2001.1806)
- 44 Herrel, A., McBrayer, L. D. & Larson, P. M. 2007 Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biol. J. Linn. Soc.* **91**, 111–119. (doi:10.1111/j.1095-8312.2007.00772.x)
- 45 Johnson, M. A. & Wade, J. 2010 Courtship neuromuscular systems across nine *Anolis* lizard species: sexual dimorphisms in structure and function. *Proc. R. Soc. B* **277**, 1711–1719. (doi:10.1098/rspb.2009.2323)
- 46 Bloch, N. & Irschick, D. J. 2006 An analysis of interpopulation divergence in visual display behavior of the green anole lizard (*Anolis carolinensis*). *Ethology* **112**, 370–378. (doi:10.1111/j.1439-0310.2006.01162.x)
- 47 Irschick, D. J., Ramos, M., Buckley, C., Elstrott, J., Carlisle, E., Lailvaux, S. P., Bloch, N., Herrel, A. & Vanhooydonck, B. 2006 Are morphology–performance relationships invariant across different seasons? A test with the green anole lizard (*Anolis carolinensis*). *Oikos* **114**, 49–59. (doi:10.1111/j.2006.0030-1299.14698.x)
- 48 Herrel, A., Van Damme, R., Vanhooydonck, B. & De Vree, F. 2001 The implications of bite performance for diet in two species of lacertid lizards. *Can. J. Zool.* **79**, 662–670. (doi:10.1139/z01-031)
- 49 Herrel, A., Spithoven, L., Van Damme, R. & De Vree, F. 1999 Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* **13**, 289–297. (doi:10.1046/j.1365-2435.1999.00305.x)
- 50 Lailvaux, S. P. & Irschick, D. J. 2007 Effects of temperature and sex on jump performance and biomechanics in the lizard *Anolis carolinensis*. *Funct. Ecol.* **21**, 534–543. (doi:10.1111/j.1365-2435.2007.01263.x)
- 51 Losos, J., Creer, B. D. A. & Schulte, J. A. 2002 Cautionary comments on the measurement of maximum locomotor capabilities. *J. Zool.* **258**, 57–61. (doi:10.1017/S0952836902001206)
- 52 Adolph, S. C. & Pickering, T. 2008 Estimating maximum performance: effects of intraindividual variation. *J. Exp. Biol.* **211**, 1336–1343. (doi:10.1242/jeb.011296)
- 53 Irschick, D. J., VanHooydonck, B., Herrel, A. & Meyers, J. 2005 Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biol. J. Linn. Soc.* **85**, 211–221. (doi:10.1111/j.1095-8312.2005.00486.x)
- 54 Kachigan, S. K. 1991 *Multivariate statistical analysis: a conceptual introduction*, 2nd edn. New York, NY: Radius Press.
- 55 Garcia-Berthou, E. 2001 On the misuse of residuals in ecology: testing regression residuals versus the analysis of covariance. *J. Anim. Ecol.* **70**, 708–711.
- 56 Lailvaux, S. P., Hathway, J., Pomfret, J. & Knell, R. J. 2005 Horn size predicts physical performance in the beetle *Euoniticellus intermedius*. *Funct. Ecol.* **19**, 632–639. (doi:10.1111/j.1365-2435.2005.01024.x)
- 57 Henningsen, J. P. & Irschick, D. J. 2012 Manipulating dewlap size reveals that performance is more important than signal size in determining the outcome of staged dominance interactions in male green anole lizards.

- Funct. Ecol.* **26**, 3–10. (doi:10.1111/j.1365-2435.2011.01893.x)
- 58 Knell, R. J. & Simmons, L. W. 2010 Mating tactics determine patterns of condition dependence in a dimorphic horned beetle. *Proc. R. Soc. B* **277**, 2347–2353. (doi:10.1098/rspb.2010.0257)
- 59 Royle, N. J., Lindstrom, J. & Metcalfe, N. B. 2006 Effect of growth compensation on subsequent physical fitness in green swordtails *Xiphophorus helleri*. *Biol. Lett.* **2**, 39–42. (doi:10.1098/rsbl.2005.0414)
- 60 Royle, N. J., Metcalfe, N. B. & Lindstrom, J. 2006 Sexual selection, growth compensation and fast-start swimming performance in green swordtails, *Xiphophorus helleri*. *Funct. Ecol.* **20**, 662–669. (doi:10.1111/j.1365-2435.2006.01147.x)
- 61 Mappes, J., Alatalo, R. V., Kotiaho, J. & Parri, S. 1996 Viability costs of condition-dependent sexual male display in a drumming wolf spider. *Proc. R. Soc. Lond. B* **263**, 785–789. (doi:10.1098/rspb.1996.0117)
- 62 Herrel, A., Joachim, R., Vanhooydock, B. & Irschick, D. J. 2006 Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biol. J. Linn. Soc.* **89**, 443–454. (doi:10.1111/j.1095-8312.2006.00685.x)
- 63 Herrel, A., James, R. S. & Van Damme, R. 2007 Fight versus flight: physiological basis for temperature-dependent behavioral shifts in lizards. *J. Exp. Biol.* **210**, 1762–1767. (doi:10.1242/jeb.003426)
- 64 Hertz, P. E., Huey, R. B. & Nevo, E. 1982 Fight versus flight: body temperature influences defensive response of lizards. *Anim. Behav.* **30**, 676–679. (doi:10.1016/S0003-3472(82)80137-1)
- 65 Leal, M. & Rodriguez-Robles, J. A. 1995 Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). *Copeia* **1995**, 155–161. (doi:10.2307/1446810)
- 66 Husak, J. F., Lappin, A. K. & Van Den Bussche, R. A. 2009 The fitness advantage of a high-performance weapon. *Biol. J. Linn. Soc.* **96**, 840–845. (doi:10.1111/j.1095-8312.2008.01176.x)
- 67 Hunt, J., Breuker, C. J., Sadowski, J. A. & Moore, A. J. 2009 Male–male competition, female mate choice and their interaction: determining total sexual selection. *J. Evol. Biol.* **22**, 13–26. (doi:10.1111/j.1420-9101.2008.01633.x)
- 68 Lailvaux, S. P. & Kasumovic, M. M. 2011 Defining individual quality over lifetimes and selective contexts. *Proc. R. Soc. B* **278**, 321–328. (doi:10.1098/rspb.2010.1591)
- 69 Irschick, D. J. & Lailvaux, S. P. 2006 Age-specific forced polymorphism: implications of ontogenetic changes in morphology for male mating tactics. *Physiol. Biochem. Zool.* **79**, 73–82. (doi:10.1086/498194)
- 70 Losos, J. B. & Chu, L.-R. 1998 Examination of factors potentially affecting dewlap size in Caribbean anoles. *Copeia* **1998**, 430–438. (doi:10.2307/1447437)
- 71 Nicholson, K. E., Harmon, L. J. & Losos, J. B. 2007 Evolution of *Anolis* dewlap diversity. *PLoS ONE*, **3**, e274. (doi:10.1371/journal.pone.0000274)
- 72 Ord, T. J. 2008 Dawn and dusk ‘chorus’ in visually communicating Jamaican anolin lizards. *Am. Nat.* **172**, 585–592. (doi:10.1086/590960)
- 73 Leal, M. & Fleishman, L. J. 2002 Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proc. R. Soc. Lond. B* **269**, 351–359. (doi:10.1098/rspb.2001.1904)