

# Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation

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According to basic evolutionary theory, individuals within a population should adapt their behavior in response to their current physical and social environment. However, there is now evidence from a diverse range of taxa that behavior is instead constrained by individuals' broad behavioral syndromes or personalities. Bold individuals are generally shown to take greater risks than shy individuals. Theory suggests that there should be fitness trade-offs associated with personalities. We aimed to answer the following 3 questions using the Namibian rock agama (*Agama planiceps*) as a study species: 1) Is the boldness of individual male agamas repeatable? 2) Do male agamas show a behavioral syndrome? and 3) Are there any possible fitness trade-offs associated with individual behavioral syndromes. We measured boldness of 30 male agamas by quantifying flight initiation distance. We found that individual agama behavior was significantly consistent through time. Also, bolder males were found to spend significantly more time basking and moving throughout their home ranges in sight of predators, indicating a behavioral syndrome in this species. Bolder males also had larger home ranges and fed more than shy males but suffered higher levels of tail loss, possibly due to predation. The rates of visual signaling in the form of assertion displays of bolder and shy males did not differ. We suggest that males of this species show a significant behavioral syndrome that may lead to fitness trade-offs. *Key words:* *Agama planiceps*, behavioral syndrome, boldness, individual variation, personality. [*Behav Ecol* 21:655–661 (2010)]

Individuals within a population should adapt their behavior to suit their current physical and social environment (Elgar 1989; Childress and Lung 2003). However, there is now evidence from diverse taxa such as birds (Carere et al. 2005; Quinn and Cresswell 2005; de Azevedo and Young 2006), mammals (Gosling 1998; Reale et al. 2000; Bremner-Harrison et al. 2004), reptiles (Lopez et al. 2005), fish (Wilson et al. 1993; Wilson and Godin 2009), and invertebrates (Mather and Anderson 1993) that this is not always the case. Indeed, it has been shown that some aspects of individual behavior are instead constrained within broad behavioral syndromes or "personalities" that can cause the maintenance of suboptimal correlations in behavior (after Sih et al. 2004, reviewed in Gosling and Vazire 2002; Dall et al. 2004; Dingemanse and Reale 2005), which can have a heritable component (Drent et al. 2003).

Contrary to predictions that flexible and responsive behavior should be selected for within a population, investigations into animal personality have found that individuals tend to vary consistently in their behavior. Although individuals' behavior may vary through time as they age, rank-order differences between individuals tend to remain consistent; for example individuals may become bolder with age, but bolder individuals will tend to stay bolder than shy individuals over time. A behavior is consistent when variation within individuals is lower than the variation among individuals for a given behavior (Sih et al. 2004; Bell et al. 2009). Measures of repeatability are thus essential in studies of personality. Repeatability of certain behaviors has been well documented in great tits (*Parus*

*major*). Both exploratory behavior and boldness were found to vary more among individuals than within individuals over multiple years (Dingemanse and de Goede 2004; van Oers et al. 2004), demonstrating the repeatability of behavior within individuals. A recent meta-analysis that investigated studies of the repeatability of behaviors found evidence that factors such as taxon and age may affect repeatability but that a range of measured behaviors are otherwise consistent through time in many species (Bell et al. 2009).

Particular personality traits involve both costs and benefits thus making it impossible for individuals to consistently behave in an optimal manner. Personality can be defined across several different axes, including boldness, aggressiveness, sociability, and activeness (Gosling and Vazire 2002). Even within one axis of personality, for example boldness, animals may not always choose the optimal behavior for the situation (Wilson and Godin 2009). For example, bolder individuals may gain greater access to resources by being more dominant (Harfmann-Short and Petren 2008; Pruitt et al. 2008) but may also incur a greater risk of predation (Dugatkin 1992; but see Godin and Davis 1995; Bremner-Harrison et al. 2004). Thus, individual variation in any axis of personality, such as boldness, may persist because there are both costs and benefits so that individuals with different levels of boldness experience benefits (and pay costs) in different ways. For example, individual variation in personality may be tied to individual variation in growth and mortality rates, with selection for higher growth rates selecting for riskier behaviors (Stamps 2007). However, the evolutionary significance of personality traits such as the boldness syndrome is still contentious (see Wilson and Godin 2009). The expression of such personality traits may be context specific (Coleman and Wilson 1998) but is often more general. Correlations among particular personality traits, termed behavioral syndromes or behavioral carry-over (Sih et al. 2004) are particularly interesting as they make it less likely that individuals' behavior will be optimal in most

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situations (Dall et al. 2004; Quinn and Cresswell 2005). For example, individual great tits that readily explored novel environments were also more aggressive, took greater risks and were better scroungers than those individuals that were less inclined to explore novel environments (Verbeek et al. 1996; reviewed in Dingemanse and Reale 2005).

To understand the ultimate causes of behavioral carryover and the maintenance of behavioral syndromes, the fitness costs and benefits of consistent behavioral differences must be estimated. For example, asocial comb-footed spiders (*Anelosimus studiosus*) are more aggressive and active than social individuals. This is posited to result in a higher rate of prey capture, thus increasing fitness; however, it may also increase the occurrence of sexual cannibalism, which presumably decreases fitness (Pruitt et al. 2008). Several theories exist about how different behavioral syndromes can be maintained, such as through frequency-dependent selection; however, measures of the costs and benefits to fitness of behavioral syndromes must be assessed before we can understand the processes that maintain variation in personality in the wild (Coté et al. 2008). These costs and benefits should first be measured in a species at a single location and time as these might vary among both sites and seasons; the next step in understanding the maintenance of behavioral syndromes would be comparisons across populations.

Individuals that signal to potential mates using olfactory, visual, or aural cues often have to trade-off the benefit of attracting a mate with the cost of attracting predators, making signaling a risk-taking behavior (Magnhagen 1991; Johnstone 1997; Mougeot and Bretagnolle 2000; Huhta et al. 2003; Searcy and Nowicki 2005; Møller et al. 2008). Lizards from varied families signal to conspecifics primarily by using color and movement (Johnstone 1997). They have a large repertoire of signaling behaviors directed at intra- and intersexual conspecifics; one of the most widespread across families is the "assertion" display (Radder et al. 2006). Assertion displays are spontaneous displays not directed at particular conspecifics or performed when there is an obvious audience. Individuals give assertion displays from elevated perches (Johnstone 1997) or when moving (Radder et al. 2006). These displays are designed to catch the attention of any local conspecifics and must be visible at long range, making them conspicuous to predators. Lizard behavior therefore provides an ideal system to investigate the consequences of bold signaling in a natural system.

Namibian rock agamas (*Agama planiceps*) provide an interesting system for investigating the costs and benefits of inter-individual differences in boldness. The Namibian rock agama is an agamid lizard endemic to rocky granite outcrops within Namibia. Like many other lizards in the genus *Agama*, male rock agamas are brightly colored, territorial, and perform assertion displays. Males bask and display on elevated perches and move throughout their home ranges while performing assertion displays. Both of these behaviors, basking prominently and moving while signaling, make agamas more obvious to predators, and hence can be classified as risk-taking behaviors. Males also spend time in crevices within their home ranges, often sitting where they are able to see out of the crevice but not be seen by aerial and possibly terrestrial predators (Carter AJ, personal observation). This behavior may be used to mitigate predation risk.

We observed wild individually identifiable male Namibian rock agamas in northern Namibia to address the following aims. 1) We assessed the repeatability of boldness in individual male agamas, predicting that males would vary along a continuum from bold to shy as has been found in previous studies of lizard personality (Lopez et al. 2005) and that individual males' reactions to a stimulus would be consistent through

time. 2) We tested the hypothesis that individual differences in boldness in male agamas would be part of a behavioral syndrome, with boldness correlated with individual differences in other aspects of behavior. Specifically, we predicted that bolder male Namibian rock agamas would spend more time basking and less time out of sight of predators and would signal more than shyer males. 3) We tested some possible fitness trade-offs in the costs and benefits associated with different personality types. In particular, we predicted that bolder males would suffer higher rates of tail loss, due to predation and/or conspecific aggression, but have larger home ranges, signal more, and feed more than shyer males.

## MATERIALS AND METHODS

### Study area and study species

The study was undertaken at Hobatere Campsite (lat 70°53'37.74"S, long 19°28'31.35"E), 70 km north of Kamanjab in northwestern Namibia. A population of the Namibian rock agama occupied the area (ca. 1.0 × 0.7 km) immediately around the campsite. We identified (see below) and studied 30 individuals; however, males were observed in 3 blocks of 10 each. The first block of 10 individuals was observed during February 2009, the second block during March 2009, and the third block during April 2009. The first block of males was observed at the end of the breeding season; males were observed courting females during this time (running in circles around females and head-bobbing). During the second and third blocks no courting behavior was observed. Thus we call February "breeding season" and March and April "non-breeding season."

### Male identification

Individual male agamas were identified using natural variations in their coloration; we found that males varied in the color of their legs (blue/black), the color of the distal third of the tail (blue/black), the color of the proximal third of the tail (blue/white), and the pattern of the change of colors between the head and the torso (from a straight line to an orange triangle). In order to validate this method of identifying lizards, we obtained a measure of interobserver reliability. Three observers together identified a group of 20 male agamas based on the above color pattern and any other identifying features. For example, males differed in the extent that their tails were intact, in scars on the body and patterns on the blue torso. After 5 days, the 3 observers searched the field site in a random order and identified males together but without consulting with each other. Observers could record the identity of a male or record the male as Unknown. Once a male in one area had been identified, the observers moved to another section of the site in order to avoid identifying males in one area by a process of elimination. We found 19 of the 20 identified males in a 2-h period. Two of the 3 observers agreed in their identification of all 19 males found, and the third observer agreed with the identities of 16 of the 19 males; the remaining 3 males she recorded as Unknown. For all males that were given an identity, all 3 observers' records of identity agreed. Two observers had no previous experience identifying Namibian rock agamas before this activity. Thus, we believe that this methodology allowed us to accurately and consistently identify agamas in the field without having to unduly stress them by catching and marking them.

### *Aim 1: repeatability of measures of the boldness of individuals*

To obtain multiple measures of the boldness/shyness of each of the identified male agamas, we measured their flight

initiation distances (FIDs). Males were measured 4–18 times each to estimate the repeatability of this measure over a short period of weeks. For males that were tested multiply in one day, there was an average of  $207.55 \pm 11.5$  min between tests ( $n = 89$ ) and no more than 4 tests per day. Most males were tested within one week. To do this, the same observer approached each individual male on foot at a constant speed (4 km/h; measured using a GPS unit [GPS12; Garmin Ltd., Olathe, KS]), and the distance from the observer at which the male fled was quantified using a 50-m measuring tape. Males were only approached when they were perched prominently within their home ranges to simulate a predator attack during a risk-taking behavior. Males perched at the top of a rock were able to flee to the other side of the rock to avoid the “predator,” and consequently, all males were at similar distances from “refugia.” We ensured that males were approached when perched on different rocks within their home ranges to account for variation in habitats that the males may have used. Individuals were not approached if they were above the chest height of the observer, if they were behind an obstruction and could not be approached directly, or if they were within 10 m of another agama (individuals are known to change their FID based on the presence of conspecifics [Cooper 1999]). Observations were not recorded if individuals moved before the observer could get into position or if there was any disturbance during the course of the FID experiment. All FID experiments were performed between 1000 and 1600 h because ambient temperature has been shown to affect the FID of ectotherms (Cooper 2000); between 1000 and 1600 h, ambient temperatures were high ( $>25$  °C) during all 3 months, and males should have been at their preferred body temperatures. To assess the repeatability of boldness over a longer period of time (months), the first group of males observed was tested multiply in February and in April.

#### *Aim 2: evidence of a behavioral syndrome*

Each male was observed by 2 observers for 10 min using continuous focal sampling techniques. Male signaling behavior can occur very quickly, thus one observer dictated behavioral state changes and behavioral events to a scribe who recorded them. The scribe sat at  $>20$  m from the home range of the male, and the observer sat at least 15 m from the male. Occasionally, it was necessary for the observer to move into the home range of the male as the male moved through it but the observer moved away as soon as possible if this occurred. Recorded behavioral states included Basking, Thigmothermy (obtaining heat from the substrate), Sitting in shade, Moving, Hiding, and Other. We considered males to be Basking when their head and torso were clear of the ground and they were sitting in the sun (and exposed to predators). We considered males to be in Thigmothermy when they had either their torso or their head and torso pressed against the substrate. We defined Sitting in shade to be when males were in the Basking position but in the shade. This generally meant that they were less visible to predators as they were under a tree or next to a ledge. We defined males to be Moving when they were locomoting. Agamas tend to run in fits and starts; as a consequence, we defined males as having stopped moving once they had stopped for 3 s. Males were considered to be Hiding when we could not see them or if we could see them but they were in a crevice/crack in the rock (at the entrance but not obviously visible to predators). Males were generally in rock crevices when they were classified as Hiding. Any behavior that did not fit into these definitions we recorded as Other. Other included all conspecific interactions (courting and dance displays such as extension of the gular flap with jerky motions of the body directed at conspecifics of the same sex) and cir-

cular walking (males “marked” their regular perches by sliding their bodies along the substrate in a circle or a figure 8). Observations were assisted with the use of a pair of binoculars (Bausch & Lomb 10 × 28) when necessary.

During focal observations, we also recorded the frequencies of a number of behavioral events. We recorded the number of times that males either head bobbed or did push-ups. As we were interested in the rate of signaling and both head-bobs and push-ups should be conspicuous movements to predators, we did not distinguish between the 2 types of signals; we refer to these behaviors collectively as signaling. We defined signaling as any movement of the head and/or torso along a vertical plane. A signaling event was recorded when such movement resulted in no net change in position of the head (i.e., head moved up and down completely).

#### *Aim 3: possible fitness trade-offs of boldness/shyness*

*Home range estimation.* Although agamas do defend territories, we were unable to confidently define all boundaries; consequently, we refer to all spatial patterns measured as “home ranges.” We quantified the sizes of the home ranges of the 30 observed males by taking GPS positions of males. To get the most accurate estimations of the home ranges of the males, an observer moved through the study site at least daily to find the study individuals. If a male was observed in a new position, the observer returned to GPS that position at a later time when the male was not there, to reduce disturbance. We also observed males for up to an hour at a time from a distance of more than 20 m away to observe any new positions that the males occupied during that time. New positions noted in this manner were recorded as mentioned above. Positions of males were taken when the accuracy of the GPS readings were 3 m or less.

*Tail loss.* A team of 3 observers moved through valleys in the field site that were not used for observations of focal individuals in order to get an independent sample with which to test for a correlation between boldness and tail loss. The observers moved slowly through each valley scanning the rocks along the sides of the valley using a pair of binoculars. When an individual male Namibian rock agama was observed, we assessed the state of the tail. Individuals were defined as having a half tail if they were missing a third or more of the tail or whole tail if they were missing less than a third of the tail or had intact tails. If the individual was a half-tail individual, we searched the immediate area within a 50 m radius to find the nearest neighbor with a whole tail. Using pairs of males in this fashion should alleviate biases in spatial heterogeneity such as habitat structure and presence of predators. The observers then moved to a position where they could approach the individuals in a direct manner from a distance of at least 15 m from the individual. The FID was recorded as above for each individual tested. We randomized the order in which half- and whole-tail males were assessed. All tests were completed on both individuals within 5 min of each other in order to control for differences in ambient temperature and done between 1000 and 1500 h so that male agamas were at their preferred body temperatures. No experiment was completed if either of the test males were disturbed during the course of the experiment nor did we include individual half-tail males for whom we could not find a near neighbor. The observers moved through each valley only once to test individuals. We are thus confident that no individuals were tested more than once for this part of the study.

*Feeding rates.* We recorded feeding events of males during focal observations. A feeding event was recorded when the observer saw a male bite and masticate an object. Males generally ate lepidopteran larvae, small orthopterans, and other insects, but we also observed males eating flowers and other soft plant material.

## Statistical analyses

### Aim 1: repeatability of measures of the boldness of individuals

We used the average of the FIDs of the focal males as a measure of boldness. Bolder males will have a shorter FID than shy males by our definition of boldness (risk taking). Average male FIDs did not vary significantly with proximity to the campsite (bordering campsite [ $n = 12$ ] =  $2.60 \pm 0.55$  m, within 50 m of campsite [ $n = 8$ ] =  $4.25 \pm 0.69$ , >50 m from campsite [ $n = 10$ ] =  $3.78 \pm 0.73$  m; analysis of variance,  $F_{2,29} = 1.76$ ,  $P = 0.19$ ), thus we did not include “campsite proximity” as a variable in the following model. Repeatability ( $r$ ) was calculated following the protocol described in Lessells and Boag (1987), and the standard error (SE) was calculated following Becker (1984).

### Aim 2: evidence of a behavioral syndrome

We investigated whether there were relationships between FIDs and the recorded behaviors using linear mixed effects (LMEs) models with “month” as a random factor and FID as the response variable. As we were interested in risk-taking behavior, and both Basking and Moving presumably attract the attention of predators, we analyzed Conspicuous Behavior as the sum of time spent Basking and time spent Moving. Proportions of time spent in each behavior were square root arcsine-transformed to break the bounds set by proportions. Time spent in Thigmotaxis was log-transformed, and the exponential of the time spent in Conspicuous Behavior was used to satisfy normality assumptions. Times spent Sitting in shade and in Other behaviors were overdispersed on analysis, thus we analyzed these data using Spearman rank correlations. Signaling was converted to a rate/time spent conspicuous, which was log-transformed to satisfy normality assumptions and analyzed as above. Data were checked for overdispersion. Data were analyzed using R (version 2.7.1 using the package “nlme”; R Development Core Team 2008).

### Aim 3: possible fitness trade-offs of boldness

**Home range size.** We used minimum convex polygons (MCPs) to estimate the home ranges of the observed males. We considered MCP estimation to be appropriate for this system as males are thought to be territorial and thus should not leave the boundaries of their home ranges once they have been established; we did not wish to overestimate their home range sizes by using other methods of analysis. MCPs were calculated using R (version 2.7.1 using the package “adehabitat”; R Development Core Team 2008). We investigated whether home range sizes of identified males related to their FIDs using a LMEs model in R (version 2.8.1 using the package nlme, R Development Core Team 2008) with month as a random factor; MCPs were log-transformed to satisfy normality assumptions.

**Frequency of tail loss.** For each pair of males, we assessed whether the whole- or half-tail male had the longer FID. We then used a  $\chi^2$ -test to compare the number of pairs in which half-tail males had longer FIDs than whole-tail males with the number of pairs showing the opposite pattern.

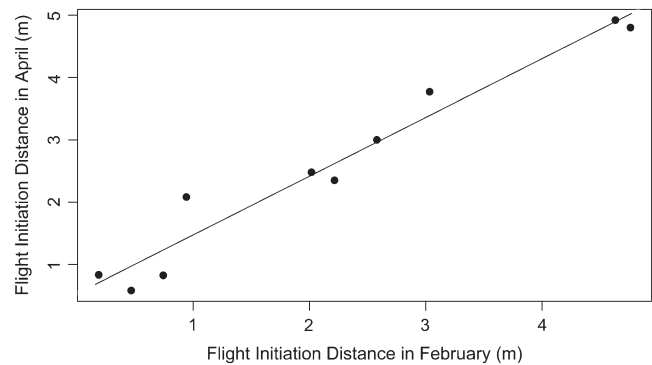
**Feeding rates.** Numbers of feeding events were converted to rates/10 min and compared with males’ FIDs using a Spearman correlation test.

Data are presented as means  $\pm$  SE.

## RESULTS

### Aim 1: repeatability of measures of the boldness of individuals

We assessed each male’s FID on average  $8 \pm 0.73$  times (range = 4–18 times). Male FID averaged  $3.14 \pm 0.39$  m (range 0.53–



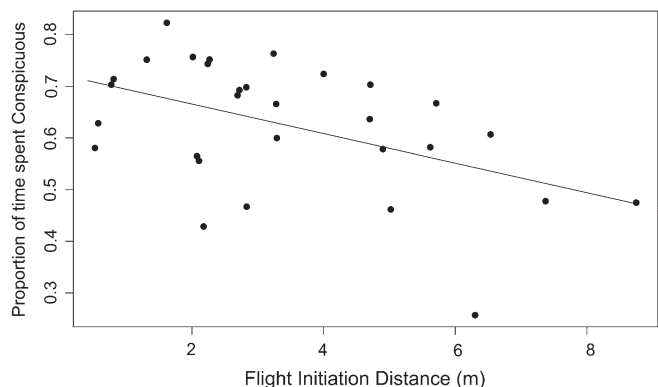
**Figure 1**

The relationship between the averages of individual males’ FIDs during February and April. The line represents the line of best fit for the regression.

8.75 m; average of each male’s average). FID did not vary significantly with time since last test within a day; thus, we believe there are no learning effects or habituation to the stimulus (LME;  $\beta \pm SE = -0.0001 \pm 0.0004$ , degrees of freedom [df] = 129,  $t = -0.30$ ,  $P = 0.76$ ). Ten males were tested during 2 periods (in February and in April) to investigate long-term repeatability of boldness. Males increased their FID in April by an average of  $0.41 \pm 0.11$  m (range 0.04–1.14 m); however, male FID was repeatable during the 2 time periods ( $r = 0.95 \pm 0.033$ ; Figure 1). Because of the difference in FIDs during the breeding and nonbreeding seasons for these males, data presented below were analyzed using the average of the February FIDs for all males observed during that time.

### Aim 2: evidence of a behavioral syndrome

We observed each of the 30 individual male agamas on average  $10.5 \pm 0.15$  times (for a total of 3350 min, range = 9–15 times). We found that males spent, on average,  $56.6 \pm 2.1\%$  of the time observed Basking,  $5.9 \pm 0.4\%$  Moving,  $28.5 \pm 2.3\%$  in Thigmotaxis,  $3.3 \pm 0.4\%$  Hiding, and  $5.7 \pm 0.7\%$  doing Other behaviors. There was a negative correlation between FID and time spent in Conspicuous Behaviors ( $\beta \pm SE = 16.63 \pm 4.29$ , df = 26,  $t = -3.87$ ,  $P = 0.006$ ; Figure 2). As expected given that males that spent more time being conspicuous spend less time hiding, there was a positive



**Figure 2**

The relationship between male FIDs and the proportion of time spent in Conspicuous Behaviors (basking and moving) (averaged across all 10-min focal observations of each male’s behavior). The line represents the line of best fit for the regression.

correlation between FID and time spent Hiding ( $\beta \pm SE = -3.28 \pm 1.12$ ,  $df = 26$ ,  $t = -2.94$ ,  $P < 0.007$ ). We did not find relationships between FID and any of the other behavioral categories tested (time spent in Thigmothermy:  $\beta \pm SE = 2.42 \pm 1.52$ ,  $df = 26$ ,  $t = 1.60$ ,  $P = 0.12$ ; time spent Sitting in shade:  $r \pm SE = 0.16 \pm 0.19$ ,  $z = 0.87$ ,  $P = 0.39$ ; time spent in Other behaviors:  $r \pm SE = -0.17 \pm 0.19$ ,  $z = -0.93$ ,  $P = 0.35$ ). Male's rates of signaling while conspicuous did not vary with FID ( $\beta \pm SE = -0.73 \pm 0.66$ ,  $df = 26$ ,  $t = 1.11$ ,  $P = 0.28$ ).

### Aim 3: possible fitness trade-offs of boldness/shyness

#### Home range size and boldness

Male home ranges averaged  $457 \pm 81 \text{ m}^2$  (range 21–1896  $\text{m}^2$ ). Home range sizes decreased with increasing FIDs (LME;  $\beta \pm SE = -62.3 \pm 27.1$ ,  $df = 26$ ,  $t = 2.30$ ,  $P < 0.03$ ; Figure 3), suggesting that bolder males had larger home ranges.

#### Tail loss and boldness

We recorded FIDs of 18 pairs of half- and whole-tail nearest neighbors. In 14 of the 18 nearest-neighbor pairs of males, the half-tail male had a shorter FID than the whole-tail male. These 14 pairs were significantly more than the 4 pairs showing the opposite pattern ( $\chi^2 = 5.56$ ,  $df = 1$ ,  $P = 0.02$ ), supporting our hypothesis that individuals with a shorter FID were at a higher predation risk

#### Feeding rates and boldness

Males ate at an average rate of  $0.35 \pm 0.07$  events/10 min. We found that FID and feeding rates were correlated using a Spearman correlation test ( $r \pm SE = -0.36 \pm 0.18$ ,  $z = 1.96$ ,  $P = 0.05$ ; Figure 4).

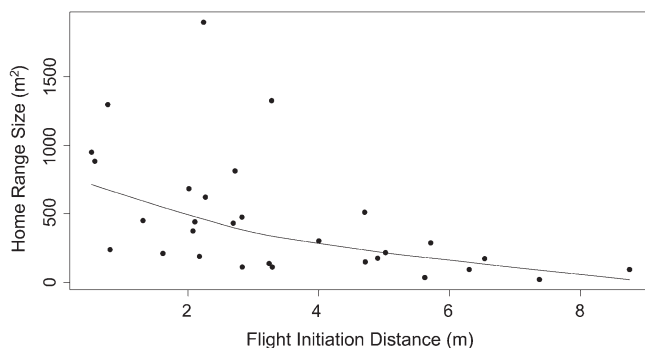
## DISCUSSION

Bolder male Namibian rock agamas spent significantly more time basking and moving and less time hiding than shyer males, suggesting a behavioral syndrome in this species. To our knowledge, this is the first time that a behavioral syndrome has been documented for a species of lizard in the wild (but see Coté et al. 2008). These data on how individuals' levels of boldness correlates with this suite of behaviors also allow us to investigate some possible trade-offs of boldness. Bolder males appeared to benefit from boldness by having larger home ranges and higher feeding rates than shyer males; however, our finding that males who had lost tails were bolder suggested that bold males also incurred costs. These observations are thus consistent with the predictions of a trade-off with boldness, although experimental manipulations would be necessary for a stronger test of this. Contrary to our pre-

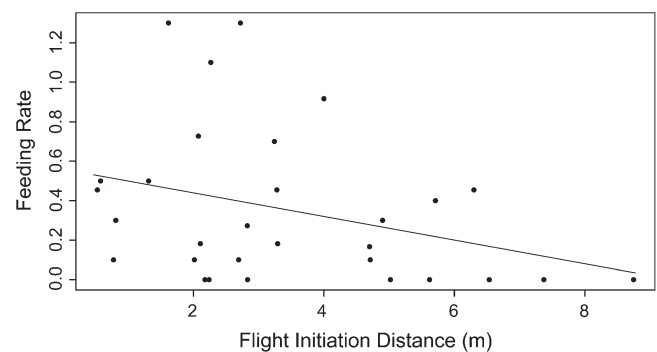
dictions, the signaling behavior of bolder and shyer males did not differ.

Before investigating the possible trade-offs of individual variation in behavior it is important to show that individual behavior is consistent. We tested the FIDs (our measure of boldness) of individuals many times and found strong repeatability in individuals' boldness levels, showing that this aspect of personality was highly repeatable in the agamas. All the males tested in both February and April had longer FIDs in April, but the bolder individuals remained bolder than the shyer ones on a rank-order basis. We observed males interacting with females during February but not in March or April. The cost to males of responding earlier to predators (having a longer FID) is presumably greater during the breeding season in terms of lost opportunities to perform fitness-enhancing activities such as territorial interactions and courting females (Cooper 1999; Cooper and Frederick 2007; Cooper and Wilson 2007). For example, Cooper and Wilson (2007) showed that male striped plateau lizards *Sceloporus virgatus* decreased their FID when in the presence of a conspecific. Similarly, male broad-headed skinks *Eumeces laticeps* decreased their FID when a conspecific male or female was present, and males that were already mate-guarding a female further reduced their FID (Cooper 1999). A similar result was found in males of a large lizard *Psammotromus algirus*; males that were guarding females decreased their FID (Martín and Lopez 1999). It is likely to be adaptive for males to trade-off higher predation risk for greater opportunities to increase reproductive success during the breeding season. However, this response seems nonetheless to be mediated by the boldness of the focal males as males that were bolder in February were also bolder in April (Figure 1).

Individuals that were missing a third or more of their tail were more likely to be bolder individuals; we thus suggest that bolder individuals may suffer a higher predation risk, making this a cost to being bold. Namibian rock agamas are preyed on by mongooses (e.g., *Galerella nigrata*; Cowley and Cunningham 2004; Rathbun and Cowley 2008), raptors such as *Falco* spp. (Braine S, personal communication), and snakes. There are 3 alternative explanations for the relationship between boldness and tail loss. 1) It is possible that individuals become bolder after a predation attempt, shortening their FIDs, based on their previous successful experience with a predator. In studies that found lizards to have shorter FIDs after tail autotomy, individuals were reported to rely more on crypsis (reviewed in Bateman and Fleming 2009). However, we did not observe male Namibian rock agamas using crypsis when being approached directly. 2) Alternatively, male agamas may



**Figure 3**  
The relationships between male FIDs and home range sizes. The line represents the line of best fit for the regression.



**Figure 4**  
The relationship between male FID and feeding rate/10 min. The line represents the line of best fit, however, data were analyzed with a Spearman correlation test ( $P = 0.05$ ).

shorten their FIDs as a response to autotomization and their decreased fitness; indeed individuals with autotomized tails suffer from reduced running speed and decreased endurance (reviewed in Bateman and Fleming 2009). Male agamas may therefore rely on other antipredator strategies, such as crypsis, that reduce their FIDs in order to avoid predation. However, most studies of FIDs of autotomized and regular tail individuals reported either no difference or greater FIDs for autotomized individuals (Bateman and Fleming 2009). 3) It is also possible that individuals lose parts of their tails in agonistic interactions with conspecifics. Male *Agama agama* whip each other with their tails during agonistic encounters and may lose their tails in that way (Harris 1964). However, we did not observe male Namibian rock agamas either tail whipping or biting at each others' tails during male–male encounters. Consequently, we believe that FID reflects the boldness of both autotomized and whole-tail individuals and that, regardless of the causes of tail loss, it represents a serious cost to bolder males. As mentioned, individuals with autotomized tails suffer from reduced running speed and decreased endurance and consequently a higher risk of predation (reviewed in Bateman and Fleming 2009). Males with shorter tails may also suffer social costs in agonistic interactions as they appear smaller or may be less attractive to mates (Bateman and Fleming 2009). We therefore believe that tail loss is most likely to reflect previous predation attempts on individuals and that bolder individuals experience higher levels of predation risk.

Bolder males were found to have larger home ranges than shy males, suggesting a possible benefit to being bold. Having a larger home range may give a male greater access to female agamas and/or resources such as insects or plant material (Melville and Swain 1999; Vanpé et al. 2009). We are quite confident that we accurately estimated the home ranges of the observed males, but there is a chance that shy males were unwilling to enter all parts of their home ranges when being observed, even from great distances. We hypothesize that shy males suffer costs from having smaller home ranges; this should be tested in future studies. We predict that bolder males have larger home ranges because they are more aggressive and consequently fight more than shy males and/or because they spend more time surveying their home range and can respond faster and more effectively to any invasion of the home range.

We also found that bolder males fed more than shy males while being observed, which suggests another possible benefit to being bold. Bolder males may find more to eat because they have larger/better home ranges or they may eat more because they are out foraging more; this also warrants further research. Boldness is often correlated with levels of aggressiveness (Verbeek et al. 1996), and aggressive males may be able to defend home ranges that produce better/more resources. Alternatively, both shy and bolder male agamas may have had the same opportunities to gain food but shy males may have been unwilling to take those opportunities in the presence of a predator (the researcher). This kind of risk-taking behavior on the part of the bolder males may represent a significant benefit to bolder males if it causes them to gain more resources.

We predicted that shy males would signal less than bolder males as signaling can be a risk-taking behavior (Zuk and Kolluru 1998) but found no correlation between boldness and signaling behavior. The majority of our study was undertaken during the nonbreeding season during which time signaling may not have been as important to males. Bolder males may signal more during the breeding season and mitigate the cost of signaling during the nonbreeding season by decreasing their rate of signaling at that time. We suggest future studies should investigate this aspect of signaling behavior.

One question that remains unanswered in the literature on individual variation in behavior is how and why consistent differences in behavior among individuals have evolved. It has been posited frequently that interindividual differences in personality have to have ecological and evolutionary significance to be maintained (Wilson and Godin 2009), but explanations for how this can occur are limited and have not been tested. Study of the evolution of boldness syndromes must address the ecological significance of boldness in field studies, perhaps followed by experimental manipulations and modeling. We found that FIDs in the Namibian rock agama are consistent through time, correlate with risk-taking and risk-mitigating behaviors in the directions predicted by theory and may affect fitness. Bolder males may have higher reproductive success by gaining access to more females and resources in their larger home ranges but may also be predated at a younger age, making their lifetime reproductive success equal to that of shy males. An alternative explanation for individual differences in boldness is that this personality trait changes with age (Wolf et al. 2007; Biro and Stamps 2008). Further research is necessary to test this as we were unable to determine the ages of individuals used in this study.

Our results demonstrate the importance of empirical research in the field of personality research. However, without long-term studies on this and other systems, we will not be able to accurately estimate the fitness of bolder and shy individuals, which would require data on survival and reproductive success. We were not able to measure the repeatability of individual differences in the behaviors of our agamas, except for FID; this would require observations to be carried out over a longer time frame and should be the subject of further work. Empirical data should thus form the basis of experimental studies in future research. We suggest that future studies should work to the following theoretical framework to determine the evolutionary and ecological significance of consistent individual differences in behavior in wild animals: 1) estimate the repeatability of behavioral variations, 2) test for behavioral syndromes, and 3) estimate the fitness consequences of these behavioral syndromes, preferably over the lifetime of the species under study.

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