Boldness, trappability and sampling bias in wild lizards

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A R T I C L E   I N F O

Many studies of animal personality are completed in the laboratory with animals collected from the wild. However, there is some concern that studies that trap individuals to perform assessments of personality may not collect a representative sample of personality types, as some individuals may be trap-shy. We investigated the relationship between boldness and trappability using males of a species of lizard, the Namibian rock agama, *Agama planiceps*, whose boldness could be assessed in the wild prior to trapping. We observed known individuals between nine and 15 times each over several weeks, which revealed that boldness consistently differed across individuals and was not influenced by factors such as body size or environmental variables. Lizards habituated to the behavioural assay, but there was no evidence of plasticity (individual differences) in the rate of habituation. As predicted, bold individuals entered the trap sooner than shy individuals and we had higher success at trapping bold individuals. Using a simple simulation model, we show that such bias leads to underestimates of effect size and reduces the power to detect correlations between behavioural traits (i.e. behavioural syndromes). We suggest that studies that trap animals for laboratory assessments of personality may consistently underrepresent the extent of personality trait variation in the populations that they sample, and recommend that future studies either develop methods for testing personality in the field that control for obvious confounding variables or make every effort to ensure minimum bias when sampling animals for use in a laboratory setting.
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Personality in animals refers to consistent individual differences in behaviour (Sih et al. 2004). Individuals show a behavioural syndrome when one or more personality traits correlate through time or across contexts (Stamps & Groothuis 2010). Cross-context correlations in behaviour have received much attention because of their perplexing nature, as behavioural syndromes often demonstrate suboptimal behaviour in one or more contexts, when animals should theoretically select the optimal behaviour in each given context (Dall et al. 2004). For example, a bold and aggressive individual may receive a benefit when competing with conspecifics over limited resources (Pruitt et al. 2008; Short & Petren 2008). However, if boldness also correlates with activity, for example, in the presence of a predator, then bold individuals may also suffer higher predation (Bremner-Harrison et al. 2004; Biro et al. 2006; Carter et al. 2010).

Many studies of animal personality are conducted in the laboratory using animals trapped from the wild (see selectional studies: Carere et al. 2005). Of course, any such study assumes that we have random samples in order for our results to be valid and without bias. However, it is possible that personality trait differences between individuals may result in systematic trapping bias, which at the very least would result in violation of statistical assumptions and could potentially impact the power of studies to detect relationships between life history, behavioural and fitness variables (Biro & Dingemanse 2009). Indeed, it seems 'trap-shy/trap-happy' individuals and differences in catchability often exist within animal populations (rabbits, *Oryctolagus cuniculus*: Sunnucks 1998; badgers, *Meles meles*: Tuyttens et al. 1999; stoats, *Mustela erminea*: King et al. 2003; collared flycatchers, *Ficedula albicollis*: Garamszegi et al. 2009; tree snakes, *Boiga irregularis*: Tyrrell et al. 2009; chickadees, *Poecile atricapillus* and *Poecile gambeli*: Guillette et al. 2010) and that trappability may correlate with certain aspects of personality (Drickamer et al. 1995; Mills & Faure 2000). In fact, several studies have used trappability or capture method as a measure of boldness and exploratory tendency (Wilson et al. 1993, 2011; Reale et al. 2000; Boyer et al. 2010).

However, we know of only one study that has directly tested whether trappability is related to boldness, and whether variation in boldness in the trapped animals is less than the variation of that

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trait for free-living animals in the wild (Garamszegi et al. 2009). Garamszegi et al. (2009) found that the negative correlation between exploration and risk taking was stronger when estimated using animals observed in the wild compared to the equivalent analysis using only data from successfully trapped individuals. In contrast, relationships between aggression and risk taking, and aggression and exploration, were weaker for wild animals than for captured ones (Garamszegi et al. 2009). Given that trappability has been found to vary with personality in birds (Mills & Faure 2000; Garamszegi et al. 2009), mammals (Reale et al. 2000; Boyer et al. 2010) and fish (Wilson et al. 1993; Biro & Post 2008), it is likely that many previous studies of personality involving animals sourced from the wild have underestimated the amount of variation present in personality traits, which in turn is likely to reduce power to detect relationships between a given personality trait and some other behavioural or life history variable. However, the theory that sampling bias may affect the outcome of laboratory studies requires further testing.

Lizards are popular study organisms for personality research (Lopez et al. 2005; Cote & Clobert 2007; Cote et al. 2008, 2010; While et al. 2009; Carter et al. 2010; Rodriguez-Prieto et al. 2010, 2011), yet nothing is known about the effects of personality on trappability in lizards. Studies often trap lizards in the wild and then transport them to research facilities for testing (but see Carter et al. 2010). Lizards are often captured by noosing (for example, Lopez et al. 2005; Rodriguez-Prieto et al. 2010, 2011), which requires an approach to within 3 or 4 m of the animal. Other reported methods of trapping or catching lizards may have similar biases (Table 1). To test the effects of personality on trappability in wild lizards, we studied the Namibian rock agama, *Agama planiceps*, which is a large, brightly coloured diurnal lizard that occupies rocky granite outcrops in northwestern Namibia. Previous research on a population of Namibian rock agamas showed that average flight initiation distances (FID, or the distance between a threat and an individual when it flees) for individual lizards in the wild ranged from less than 1 m to greater than 8 m (Carter et al. 2010). Thus, noosing in this population would result in samples biased towards the bolder individuals that allow researchers close enough to noose them.

To investigate how boldness may affect trappability in this lizard species, we measured the latency of individuals to enter a trap. Our aim was to investigate the relationship between boldness and trappability in this species, and its implications for studies of lizard species in the wild versus the laboratory. We predicted that bolder individuals would be more likely to enter the trap, and would exhibit shorter latencies to do so, independent of weight or condition. We also explored the effect of personality-biased trapping/catching on the size of correlations between behavioural traits using a simulation model.

METHODS

Study Species and Study Area

The study was completed at Hobatere Campsite (70°53′37.74″S, 19°28′31.35″E), 70 km north of Kamanjab in northwestern Namibia. This population of rock agamas was the focus of a previous study that documented a behavioural syndrome in this species, whereby bolder individuals (those with low FID) spent more time conspicuous (basking and moving) than shyer individuals (Carter et al. 2010). For the current study a total of 45 male rock agamas were identified, 32 of which were followed throughout October to early December 2010 as part of a behavioural study; however, we attempted to trap only 21 of the 32 focal individuals and data for those lizards are analysed here. Male rock agamas can be distinguished from females and juveniles by their coloration: males have orange heads and tails and a blue body while females and juveniles are mottled olive-brown with a yellow and black reticulated pattern on the head and orange patches behind the shoulders. Males were individually identified using natural variation in their coloration and other identifying factors such as scars and limb/digit loss. This method has proven successful in the past (Carter et al. 2010) and avoids the stressful procedure of marking them. The study was done with permission from the Ministry of Environment and Tourism in Namibia and was approved by the Australian National University's Animal Experimentation Ethics Committee.

Measuring Boldness

The boldness of individual male agamas was assessed by measuring males' FIDs. To do so, a single observer (A.J.C.) approached each male on foot at a constant speed (4 km/h, measured using a GPS unit, eTrex, Garmin, Olathe, KS, U.S.A.) after an initial 10 min observation period. Males were observed during

Table 1
Reported methods for catching/trapping individual lizards from the wild for marking or laboratory studies, potential biases and ways to mitigate the bias from these methods

Trapping method	Potential effect of bias	Potential bias due to personality	Potential ways to mitigate bias	Example of studies that have used the method to catch lizards
Hand catching	High	Personality-dependent antipredator behaviour	Increase effort for shy individuals, attempt different trapping methods for shy individuals	Olsson et al. 1997; Chapple & Keogh 2006; Webb et al. 2008
Noosing				Smith & Griffiths 2009; Scheelings & Jessop 2011
Meal worming				Chapple & Keogh 2006
Trapping		Personality-dependent novel-object reactions	Leave the object in the environment until individuals can habituate to its presence	Gardner et al. 2007
Hand catching from crevices		Personality-dependent refuge/roost preferences	Ensure effort is made to target specific individuals to avoid those that use particularly deep/difficult refuges/roosts	Gardner et al. 2007
Hand catching diurnal lizards at night				Tolley et al. 2010
Glue/sticky traps		Personality-dependent novel-object reactions	Leave the object in the environment until individuals can habituate to its presence	Glor et al. 2001; Ribeiro et al. 2008
Pitfall traps	Low			Enge 2001
Funnel traps				Enge 2001
Burlap bands		Theoretically no bias		Sutton et al. 1999
Cover boards				Horn & Hanula 2006

this interval from outside their home ranges and from a minimum distance of 15 m. Males were only approached to test their FID when the observation period ended with the male basking prominently within his home range (following Carter et al. 2010). The distance from the observer when the male fled was measured to the nearest 5 cm using a measuring tape. We observed 21 males for the trappability analyses, and assessed their FID between nine and 15 times each (mean = 12 observations per animal, yielding a total of 244 observations). A further 24 males were identified in the study area and their FIDs were estimated in the same way resulting in 45 males whose FID was assessed between one and 15 times (mean = 9 observations per animal, yielding a total of 406 observations).

Observations began in late October (range 24 October to 4 November across individuals, mean = 26 October) and were evenly spaced over the duration of the experiment which lasted from 25 to 48 days (see Fig. 1). Observations were semirandomly stratified within days; we endeavoured to observe every male within all 2 h time blocks between 0700 and 1900 hours; however, the order in which the males were observed and tested was randomized. Because environmental conditions can change during this interval, and even within days, we measured time of day of the observation (a surrogate of air temperature), and also collected actual temperature data for a considerable subset of the observations (however, the temperature meter failed on many occasions). In addition, we noted the 'season' as the day that the first rains appeared on the landscape. Observations that fell before the first rains (15 November) were recorded as 'pre-' rainy season and those after the first rains were recorded as 'during' the rainy season.

Trapping of Agamas

All 21 male agamas were targeted for trapping using a clap trap (45 × 45 cm). Clap traps (or clap nets) consist of two sides of netted mesh that close together when sprung, trapping the individual between the two sides of netting. The trap was baited with either 15–25 Dipteran larvae collected from a carcass and placed on

a petri dish, or with one mealworm, *Tenebrio molitor*, larva (the use of different bait types did not affect our findings: see below). Clap traps baited with Dipteran larvae were sprung by the researcher using a string attached to the release mechanism; otherwise the trap was automatically sprung when the agama bit at the mealworm larva. Six agamas were trapped using the mealworm bait while 15 were trapped with the Dipteran larvae bait. The bait represents a very large meal for the agamas whose usual food is plant material and small Hymenopterans (<0.5 mm long black ants). Thus we feel that the benefit of the bait should have outweighed any 'hunger effects' that could arise because of potential satiation related to the time of day of capture. The clap trap was positioned at the base of a rock or ledge that the target agama was occupying. Most agamas moved away from the observer into a crevice or the other side of the rock as the trap was set, but soon emerged as the observer retreated (usually within 30 s, on one occasion ca. 60 s). If the agama moved away from the trap, however, the trap was repositioned closer to the agama. We attempted to capture each male on a day when it was found to be perched on an appropriate rock, but we moved the trap up to three times if the male moved away from it once it was set. Thus, the trap was always positioned 1–2 m from the agama when perched, and all but two agamas returned to the perch after the trap had been set. The researcher waited 10 m away and at 50–90° from the trap (depending on topography). Trapping began at approximately the midpoint of the behavioural sampling (4 November), and traps were set between 0815 and 1100 hours and between 1600 and 1730 hours. Males started basking by 0700 hours and would have reached preferred body temperatures by 0800 hours. Traps were not set between 1100 and 1600 hours as ambient temperatures were high (>35 °C) and males retreated to crevices to thermoregulate.
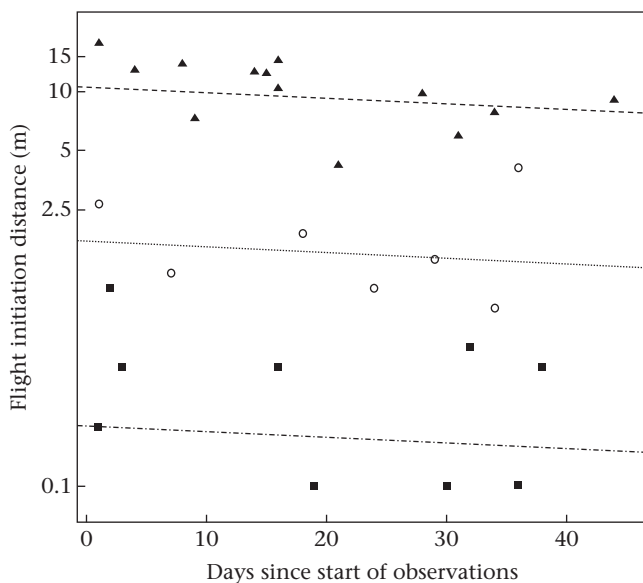
We measured two aspects of trappability: the latency to enter the trap and the probability of capture. Latency was measured as the duration from first approach to entering the trap. Agamas were recorded as approaching the trap when they oriented their body towards it, turned their head to focus one eye on it and moved towards it. All agamas showed this stereotyped behaviour when they first noticed the bait in the trap. Individuals were recorded as having entered the trap when their fore and hindlimbs were on the trap surface.

Two targeted agamas never approached the trap as they did not come close enough to see the bait. These males often displayed long FIDs (>10 m) and would not approach the researcher as she stood at a distance of 10 m from the trap (that is, they would not move to the side of the rock on which the bait was positioned) for a period of 15 min. Hence, these individuals could not be trapped and therefore no latency was recorded. We successfully trapped 15 agamas, allowing us to measure (snout–vent lengths, to the nearest mm) and weigh them (to the nearest g, using a Pesola 50 g spring scale). Males were released immediately after measurements were taken and no male was handled for longer than 180 s. One targeted individual that did not enter the trap may have been disturbed by the camp manager and his dog passing within 15 m and thus we have not included this male in the study. One male, although trapped successfully, was small enough to slip through the netting of the trap, and three other males entered the traps but the traps failed to trap them (thus we had no size measures for these).

Figure 1. Behavioural reaction norms for three Namibian rock agamas, showing flight initiation distance in relation to days since the beginning of the study. Data and reaction norms are shown for one of the shyest individuals in our sample (filled triangles, dashed line), an intermediate animal (empty circles, short-dashed line) and one of the boldest individuals (filled squares, dot-dashed line).

Statistical Analyses

Effect of individual characteristics on trappability

We analysed data according to its longitudinal nature (repeated observations over time) using general linear mixed-effects models (see Singer & Willett 2003; West et al. 2011). We used the days

since the first observation as our principal variable of interest to quantify any systematic changes in FID over time (e.g. habituation or sensitization) while also controlling for the effects of any potentially confounding variables (i.e. 'covariates'; these included ambient air temperature, time of day, season, effect of trapping and lizard mass). The effect of trapping was specified as a coded 'dummy' variable identifying pre- and post-trapping behavioural observations; season was similarly coded as pre- and during rainy season. We began with a fully saturated model containing all fixed factors (intercept, observation day and the 'covariates'). To test for individual differences in average FID, changes in individual differences in FID over time and individual differences in response to trapping, we specified the intercept, observation day and the effect of trapping as random effects, respectively. Specifying these effects as random fits a parameter describing the population mean and a variance parameter describing variation across individuals for that parameter (see Singer & Willett 2003; West et al. 2011). This method generates predictions for individual-specific intercepts and slopes (i.e. the so-called 'BLUPs', best linear unbiased predictors). Note that this method generates individual-specific predictions, but does not fit individual-specific parameters. We arrived at the final best model by sequentially culling one at a time factors that were not significant ($P > 0.1$), starting with those with the largest P value (Crawley 2005). All analyses were implemented using SAS's 'Proc Mixed', where fixed factors are evaluated using F tests, random effects tested using z tests (which are conservative relative to likelihood-based assessment), the Kenward–Roger method to calculate degrees of freedom for the fixed effects, and a type III sums of squares approach (SAS Institute, Cary, NC, U.S.A.). FID was ln transformed to normalize the data.

Upon running the models, we found the only significant factors were observation day and the random intercept effect, yielding the following final model: FID = intercept + observation day. Consequently, we used BLUP estimates of intercepts as our estimate of an individual's behavioural type (BT) for the personality trait 'boldness'. Individuals with a bolder behavioural type will have smaller BLUPs than shyer individuals. Repeatability (r) was estimated as the variance in individual intercept values as a proportion of the total variance ($var_{int}/var_{int} + var_{resid}$; Singer & Willett 2003). Repeatability tells us the proportion of variance accounted for by individual differences and is a measure of consistency.

The BT values were then used to relate to the latency to enter the trap using standard linear regression. For this analysis we used log-transformed latency values and back-transformed values of the individual-specific FID values to linearize the data; we also tested for an effect of bait type within this model. Because some researchers have questioned the use and application of BLUPs (owing to their potentially broad uncertainty), we also re-ran the final mixed model but added latency to enter the trap as a predictor within the same model (FID = intercept + observation day + trap_latency; whereby the intercept was specified as random). Finally, we also tested whether FID differed between individuals that were trapped and those that were not, using Welch's ANOVA for data with heterogeneous variances (SAS Institute).

Effect of personality-related trapping bias

If personality-biased trapping/catching of individuals does occur, this may affect relationships between behavioural traits, or between behavioural traits and other traits of interest, for any laboratory study. For example, in this study no individuals with an FID over 4 m could have been noosed (longest telescopic noosing handle is 4 m), and no individuals with an FID over 10 m were trapped. For the 45 individuals in the study area for which we identified and assessed FIDs, we calculated each individual's average FID. Although the majority of individuals had average FIDs

of less than 4 m (62%) and considerably more had FIDs of less than 10 m (91%), this still leaves approximately 40 and 10% of the population, respectively, that would not be represented in a laboratory study (Fig. 2). To understand the potential implications of this bias, we ran a simulation model in R version 2.13.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org) to evaluate the effects of such a bias on the relationship between time spent conspicuous (TSC) and FID previously determined entirely from field observations (bolder males spent significantly more time basking and moving, and thus conspicuous to predators, than shyer males; Carter et al. 2010). This would simulate the scenario in which we might instead have noosed or trapped animals from the field, and then introduced them to field enclosures for study, as has been done in previous studies (Lopez et al. 2005; Rodriguez-Prieto et al. 2010, 2011).

We used the relationship TSC = $c + \beta_0 \times$ FID + e, where c and β_0 are standard regression parameters, and e the residual variance (Carter et al. 2010). First, we simulated 200 individuals, whereby each was given a value for FID that followed a standard normal distribution. Using this population of 200 individuals, we entered these FID values into the equation describing the relationship between TSC and FID from Carter et al. (2010) to generate TSC values for each value of FID; to do so, we set c as 0, and specified the variance $e = 0.25$. Then we used those new data to calculate the estimated effect size (slope) of the relationship between TSC and FID for this 'population'. Second, we investigated the effect of sampling bias on this effect size estimate by nonrandomly sampling individuals from the population, first by sampling from the boldest 20% of the population, then increasing the trappable population in 5% increments up to 100% trappability. For each percentage of the trappable population, we randomly selected 30 individuals and ran the linear model to calculate the estimated effect size of the relationship (the slope). For example, when 50% of the population was trappable, we selected 30 individuals from the boldest half of the population, calculated the slope, and repeated this 100 times to get an average and 95% confidence interval, CI.
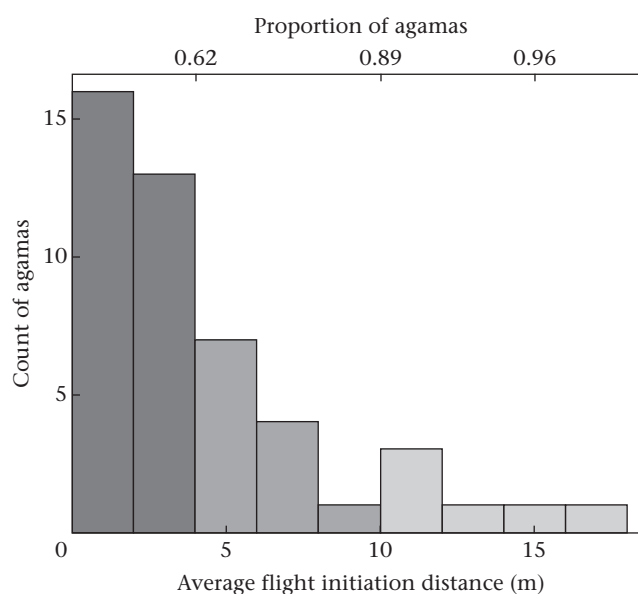
Figure 2. Frequency distribution of the average flight initiation distances for the entire population of 45 male agamas in the study area. Superimposed upon that distribution is the expected proportion of the population that would be trapped/caught using different methods of trapping/catching; dark grey bars represent those vulnerable to noosing methods, grey bars represent those vulnerable to trapping as employed in this study, and light grey bars represent those that are not catchable.

RESULTS

Behavioural Consistency Over Time

We observed that lizards displayed significant and consistent individual differences in the distance at which they took flight from an approaching observer, a measure of boldness. Some individuals took flight at great distances (up to 18 m away), whereas others allowed us to approach to within a few tens of centimetres (Fig. 2). FID was unaffected by any of the covariates (temperature, time of day, lizard mass, trapping history or season; all $P > 0.1$). However, there was evidence of habituation to the approaching observer, as FID distance declined over time on average ($F_{1,225} = 4.35$, $P = 0.04$). There was no evidence to suggest that individuals differed in the rate of habituation (random slope effect $P > 0.1$), but individuals did differ significantly in their average FID (random intercept effect: $P < 0.001$; Fig. 2). No other random effects were significant ($P > 0.1$). Repeatability of this behaviour was rather high, indicating that most of the behavioural variance could be explained by individual differences ($r = 0.71$; variance in intercept = 1.39, SE = 0.46; residual variance = 0.58, SE = 0.055).

Effect of Behavioural Type on Trappability

There was substantial variation in the latency to enter the trap, with some entering very quickly and others taking up to 600 s (mean ± SE = 100 ± 36 s, range 10–545 s), but two males did not approach the trap during the trial. Using the behavioural type estimates from the analysis of consistency above, we observed that bold individuals entered the trap more quickly than shy individuals ($r = 0.82$, slope = 0.33, $F_{1,17} = 35.6$, $P < 0.0001$; Fig. 3). There was no effect of bait type on latency to enter the trap ($P > 0.6$).

When we employed an alternative analysis using latency to capture as a predictor in the mixed model, habituation in FID was no longer detected ($F_{1,201} = 2.69$, $P > 0.10$), but FID was positively related to latency to enter the trap ($F_{1,16.6} = 8.81$, $P = 0.009$). In this model, repeatability of behaviour was also significant, but assessed as lower than in the preceding analysis ($r = 0.54$, random intercept effect: $P = 0.005$). When we considered the two males that did not approach the trap at all during the trial, we found that those males had significantly greater FIDs than those that were trapped ($F_{1,18.0} = 72$, $P < 0.001$). However, one should treat this last result with some caution given the small sample sizes involved.
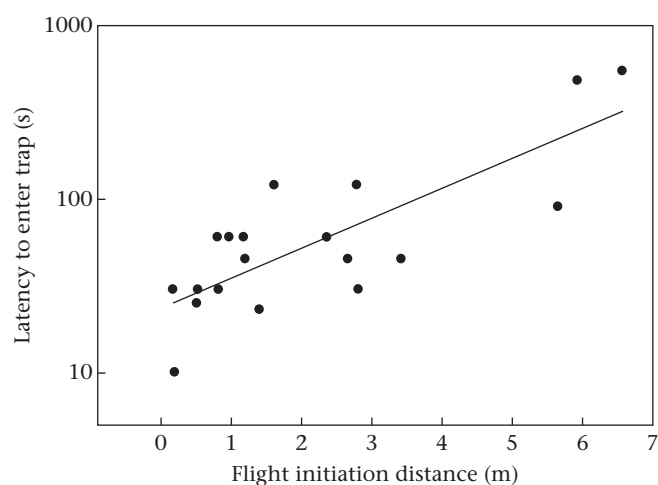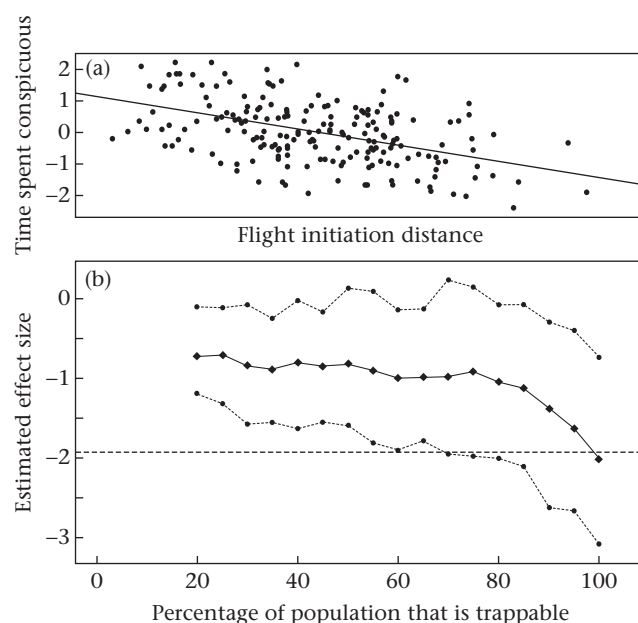

Figure 3. The relationship between male boldness and latency to enter a trap for 19 individuals that entered the trap. Low values for flight initiation distance indicate bolder males. The line represents the line of best fit for the data.

Implications of Sampling Bias for Studies of Behavioural Syndromes

Our simulation model showed clearly the likely ramifications for behavioural studies that nonrandomly sample individuals according to personality. The 'true' population effect size (actual β_0) was only reached within 95% CI when more than 60–70% of the population was trappable. Furthermore, the average estimated effect size only started approaching the actual effect size when more than 90% of the population was trappable (Fig. 4).

DISCUSSION

Our study provides several lines of evidence in favour of the idea that animal personality can affect trappability/catchability, and that the bias this introduces into behavioural studies using sampled animals can considerably impact upon their results. First, we observed consistent individual differences in flight initiation distance from an approaching threat (the observer), suggesting that individuals differ in terms of the personality trait 'boldness' and can thus be classified with a behavioural type. Second, these differences in boldness across individuals affected the latency to approach live food in a trap, and whether or not it was trapped, in short-term trapping trials. In fact, two animals were not sampled by traps and these were the two shyest animals, indicating personality-related sampling bias. Third, we showed via simulation that this sort of sampling bias may greatly underestimate the effect size of correlations between behavioural traits. These results have important implications for animal personality studies on lizards where individuals are caught from the wild in traps, or by noosing, fishing or hand catching (Lopez et al. 2005; Rodriguez-Prieto et al. 2010, 2011; see also Table 1). Below, we elaborate on these three points, and discuss the implications for studies of lizards, and the

Figure 4. The relationship between boldness and risk-taking behaviour estimated using nonrandom sampling according to simulated boldness. (a) Data for 200 simulated individuals and the estimated effect size of the relationship between flight initiation distance and time spent conspicuous. (b) Results of the simulation. The dashed line represents the estimated effect size from the simulated data in (a). The filled circles and solid line represent the average estimated effect size from 100 bootstraps for different proportions of the population being able to be sampled. The long-dashed line and small filled circles represent the upper and lower confidence intervals of the effect size estimated using boot-strapping methods.

much wider implications for any study that uses animals sampled from the wild.

FID was found to be highly consistent within individuals over a period of almost 50 days. In fact, our observed repeatability of 0.71 sits among some of the highest values reported for behavioural traits (Bell et al. 2009). This behaviour was independent of other covariates such as body mass, temperature and time of day suggesting that this personality trait was not state dependent, at least during the period when we observed the lizards. All individuals demonstrated a small but significant decline in FID with time, however, which is suggestive of habituation to the observer's approaches over the course of the study. Although FIDs decreased with time, individuals did not differ in the rate of habituation (i.e. there was no evidence for interindividual behavioural plasticity). In a similar study on Iberian wall lizards, *Podarcis hispanica*, that investigated the effect of habituation on FID, habituation was found to vary with exploration but not boldness (Rodriguez-Prieto et al. 2011). Given our relatively large number of behavioural assays (between eight and 15 observations per individual), it does not seem likely that interindividual behavioural plasticity was present, but went undetected (see also Fig. 1; Martin et al. 2011).

We found that shy individuals required more time to be caught (i.e. had longer trap latencies) and that trapping success was influenced by the boldness of the agamas; the shyest individuals were not caught. The untrapped individuals, because of their very long FIDs, were unable to be approached as closely by the researcher when the trap was being set, and were also unwilling to approach the trap area subsequently, probably because of the presence of the researcher (for ethical reasons, we remained in the trapping area while the agamas investigated the traps). However, it is possible that these individuals would eventually have noticed the bait and entered the trap if the researcher had not been present. We have previously attempted to noose Namibian rock agamas, but found that individuals with even modest FIDs (less than the average for the population) were difficult to approach within the distance needed for the noose to be used (Fig. 2). Thus, although the sample of uncaught individuals in this study is small and the bias seemingly not severe, the distribution of FIDs of the entire ($N = 45$) sample of agamas indicates that rather severe bias would have been the result had we used noosing to sample our agamas (Fig. 2).

To determine what effect trapping bias may have on the results of laboratory studies investigating the correlation between two personality-dependent behaviours, we ran a simple simulation model. This exercise revealed that as trapping bias increases in a subsample of a population, the probability of detecting the 'true' correlation decreases. Furthermore, this model shows that the true correlation will not be estimated 95% of the time until greater than 70% of the population is trappable. In addition, even when 80% of the population is sampled, the estimated effect size is almost half of the true effect size on average (Fig. 2). In this study, approximately 62% of the population would be catchable using noosing methods (Fig. 2); had we investigated the relationship between time spent conspicuous and FID in the laboratory with a noosed subsample of agamas, we would not have estimated the true population effect size because of trapping bias.

The results of this and other studies showing a trappability–boldness relationship have implications beyond those of personality studies. Trapping individuals is important for studies of population biology, pest reduction and species reintroduction (Boyarski et al. 2008). In the case of population biology, estimated population size estimates, and long-term population trends may be affected by the presence of personality-dependent sampling bias if only certain proportions of the population are trapped/recaptured (Burnham & Overton 1978; Biro & Dingemanse 2009). For example, Wanger et al. (2009) estimated the population size of giant day

geckoes, *Phelsuma madagascariensis grandis*, using a capture – mark–recapture method based on sightings of known individuals in an enclosed population. They found large individual variation in the probability of detection, with many individuals having a sighting probability close to zero. This may have been caused by differences in boldness of the individuals in the enclosure; shyer individuals may have been unwilling to stay near the transect paths in close proximity to humans or may have fled before they could be detected by the observer. In the case of pest reduction, there is circumstantial evidence that the culling of badgers resulted in artificial selection for trap-shy individuals in the culled population (Tuyttens et al. 1999), making it difficult or even impossible to eradicate a pest species. It is conceivable that through time, heavily persecuted species may show a population-wide personality shift compared to populations left alone. For example, bolder, faster-growing fish have been shown to be harvested at three times the rate of shyer, slower-growing fish (Biro & Post 2008), and differential vulnerability to angling can result in shifts in both behaviour and physiology (Cooke et al. 2007). In the case of species reintroduction, boldness has been shown to affect the survival probability of reintroduced individuals (Bremner-Harrison et al. 2004; McDougall et al. 2006); however, little attention has been paid to the trappability of the source or reintroduced populations. For example, where individuals are trapped from the wild and translocated to establish a new population (Pople et al. 2001), the new population may have higher than average boldness and take greater risks, resulting in the lower survival of these individuals and reducing the likelihood of population establishment (Bremner-Harrison et al. 2004). Finally, because many traits may be closely correlated with aspects of animal personality, the bias we demonstrate here could affect laboratory studies of cognition, endocrinology, metabolism and life history (Biro & Stamps 2008; Sih & Bell 2008; Careau et al. 2010; Coppens et al. 2010; Koolhaas et al. 2010; Stamps & Groothuis 2010; Carere & Locurto 2011).

We strongly recommend that researchers who sample wild animals carefully consider the trapping method they use to minimize bias. In the case of lizards, there are a number of methods of trapping and catching, many of which require individuals to be bold to be caught (Table 1). For example, hand capturing, noosing and fishing (Blomberg & Shine 2006; Horn & Hanula 2006; Davis et al. 2008) require individuals to have short FIDs. All methods that require a specific novel mechanism, such as pitfall traps with a drift fence, funnel traps and even glue/sticky traps (Crosswhite et al. 1999; Blomberg & Shine 2006; Ribeiro-Junior et al. 2006) will elicit novel-object reactions from the study species, which are also likely to depend on individual personality. To avoid nonrandomly sampling individuals, we suggest that specific individuals be targeted and researchers invest the necessary extra effort in catching trap-shy individuals. For example, in this study we aborted an attempt to trap an individual if it had not noticed the bait within 15 min; in the future we could set no upper limit, or attempt to catch males over consecutive trapping trials, allowing males to habituate to the traps. Habituation to a threat was found to depend on exploration tendency but not boldness in one species of lizard (Rodriguez-Prieto et al. 2011), suggesting that some shyer individuals may be trappable if given more time to habituate to a trap. Alternatively, trapping methods that involve leaving an object in the environment as a shelter, such as cover boards (Sutton et al. 1999) or burlap bands (Horn & Hanula 2006), where the study population is left to habituate to the novel object and then captured later, may more evenly sample the study population's personality types. Finally, employing two or more sampling methods can help to ensure both bold and shy individuals are caught (Biro & Dingemanse 2009; Wilson et al. 2011). To assess the generality of personality studies using wild-caught specimens in the laboratory,

we recommend that future studies explicitly list the trapping methods used and develop methods to assess personality in both the laboratory and the field to check that the study has trapped a representative sample of the population's personality types.

Acknowledgments

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