

**Sex-specific trade-offs and compensatory mechanisms: bite force
and sprint speed pose conflicting demands on the design of geckos
(*Hemidactylus frenatus*)**

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22 **Summary**

23 One of the more intuitive viability costs that can result from the possession of exaggerated
24 sexually selected traits is increased predation pressure due to reduced locomotor capacity.
25 Despite mixed empirical support for such locomotor costs, recent studies suggest such costs
26 may be masked by compensatory traits that effectively offset any detrimental effects. In this
27 study, we provide a comprehensive assessment of the locomotor costs associated with
28 improved male-male competitive ability by simultaneously testing for locomotor trade-offs
29 and potential compensatory mechanisms in territorial male and non-territorial female geckos.
30 Fighting capacity and escape performance of male Asian house geckos (*Hemidactylus*
31 *frenatus*) are likely to pose conflicting demands on the optimum phenotype for each task.
32 Highly territorial and aggressive males may require greater investment in head size/strength
33 but such an enhancement may affect overall escape performance. Among male geckos, we
34 found that greater biting capacity due to larger head size was associated with reduced sprint
35 performance; this trade-off was further exacerbated when sprinting on an incline. Females,
36 however, showed no evidence of this trade-off on either flat or inclined surfaces. The sex
37 specificity of this trade-off suggests that the sexes differ in their optimal strategies for dealing
38 with the conflicting requirements of bite force and sprint speed. Unlike males, female *H.*
39 *frenatus* had a positive association between hind-limb lengths and head size, suggesting that
40 they have utilised a compensatory mechanism to alleviate for the possible locomotor costs of
41 larger head sizes. It appears that there is greater selection on traits that improve fighting
42 ability (bite force) for males but it is viability traits (sprint speed) that appear to be of greater
43 importance for females. Our results emphasise that only by examining both functional trade-
44 offs and potential compensatory mechanisms is it possible to discover the varied mechanisms
45 affecting the morphological design of a species.

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50 **Key-words** Bite force, compensation, *Hemidactylus frenatus*, performance, sprint speed,
51 trade-off.

52 **Introduction**

53 Sexual selection is considered the dominant mechanism by which exaggerated sexual traits
54 exhibited by males of many species are shaped (Andersson, M., 1994; Berglund et al., 1996).
55 The evolution of these traits is driven by a trade-off between the benefits accrued to
56 reproduction and the costs incurred due to decreased viability. Reproductive success can be
57 enhanced by the benefits conferred to a male's competitive advantage over other males and
58 increased attractiveness to females (Andersson, S., 1994). The viability costs of exaggerated
59 traits are expected to occur via increases in development and maintenance costs and/or
60 compromised survival (Moller and Hedenstrom, 1999; Lopez and Martin, 2002; Oufiero and
61 Garland, 2007; Husak et al., 2011; Husak and Swallow, 2011). One of the more intuitive
62 viability costs for bearing enlarged sexually selected traits is increased predation pressure due
63 to either greater conspicuousness or decreased locomotor performance (Lailvaux and
64 Irschick, 2006; Oufiero and Garland, 2007; Husak and Swallow, 2011). This is because
65 sexual selection may exaggerate such traits beyond the optimum phenotype with respect to
66 biomechanical and/or physiological function, therefore imposing a cost of reduced locomotor
67 performance (Oufiero and Garland, 2007). Despite the logic underlying this mechanism,
68 surprisingly few studies provide compelling evidence that the morphological traits that
69 enhance reproductive success actually lead to quantifiable decreases in locomotor function
70 (Oufiero and Garland, 2007). For example, the exaggerated fin ornaments of male fish are
71 associated with both poorer swimming performance for some species and improved
72 swimming for others (Ryan, 1988; Basolo and Alcaraz, 2003; Royle et al., 2006; Wilson et
73 al., 2010). For example, male sword length was actually positively associated with burst
74 swimming performance for *Xiphophorus nigrensis* (Ryan, 1988), but did not affect
75 swimming endurance for *X. helleri* (Royle et al., 2006).

76
77 The lack of convincing empirical evidence for the locomotor costs of exaggerated male traits
78 may be due in part to other unmeasured traits that effectively compensate for the negative
79 impacts on locomotor function and mask their detection (Moller, 1996; Oufiero and Garland,
80 2007; Husak and Swallow, 2011). Central to this idea is that selection rarely acts on a
81 bivariate relationship between a sexually selected trait and performance in isolation (Lande,
82 1980; Arnold, 1983; Irschick and Le Galliard, 2008), but rather on the complex interactions
83 among traits (Vanhooydonck et al., 2001; Van Damme et al., 2002; Calsbeek, 2007; Calsbeek

84 and Irschick, 2007). Therefore natural selection may cause modifications of other traits to
 85 counteract the negative effects of sexually selected traits, or ‘compensatory traits’
 86 (Kirkpatrick, 1987; Moller, 1996; Oufiero and Garland, 2007; Husak and Swallow, 2011).
 87 Support for such compensatory traits derives from several studies examining the relationship
 88 between male ornaments, locomotor function and morphological variation in both birds and
 89 insects (Moller, 1996; Husak and Swallow, 2011). For example, Husak et al., (2011) found
 90 that for those species of stalk-eyed flies in which the males possessed wider eye-spans than
 91 females, the males also possessed greater relative wing areas. The presumed benefit for
 92 possessing greater wing areas, and thus the compensatory mechanism, is the ability to
 93 maintain good flight performance despite the potential negative impacts of exaggerated eye-
 94 stalks (Husak et al., 2011). However, it is unclear if such compensatory mechanisms are
 95 widespread among other organisms that possess exaggerated sexually selected structures, or
 96 if such mechanisms only act on traits selected for by females rather than via male-male
 97 fighting ability (Lailvaux and Irschick, 2006).

98
 99 Many lizard species engage in male-male combat for access to resources or mates; typically,
 100 fights are based on gaping-mouth displays, chasing and biting. In these animals, sexual
 101 selection on the underlying functional trait (bite force) could indirectly cause selection for
 102 larger head sizes, compromising locomotor function (Anderson and Vitt, 1990; Lopez and
 103 Martin, 2002; Huyghe et al., 2005; Husak et al., 2006a; Vanhooydonck et al., 2010). For
 104 example, fighting capacity and escape performance are likely to rely upon different suites of
 105 morphological traits, potentially placing conflicting demands on an individual’s phenotypic
 106 design which may lead to evolutionary or functional trade-offs (Lewontin, 1978; Garland and
 107 Carter, 1994; Vanhooydonck and Van Damme, 2001). Highly territorial lizard species may
 108 provide a good model of this functional trade-off, as intrasexual competition may require a
 109 greater investment in bite-force performance and thus head size, which may in turn affect
 110 overall manoeuvrability and speed of an individual (Lopez and Martin, 2002). Thus, the
 111 conflicting demands on an individual’s phenotypic design can result in a compromised
 112 phenotype where one motor task is afforded higher performance at the expense of another, or
 113 may be compensated by mechanisms that counteract any reduced performance.

114

In this study, we examined potential trade-offs between those performance functions important to fighting ability (e.g. bite force) and locomotor performance in Asian house geckos (*Hemidactylus frenatus* - Duméril & Bibron, 1836), and tested whether compensatory mechanisms may obscure the detection of such potential locomotor costs. *Hemidactylus frenatus* is an urban-generalist inhabiting most tropical regions worldwide and is rarely seen on the ground, preferring vertical walls and roofs (Hoskin, 2011). Importantly, this gecko is also highly territorial, and males engage in intense agonistic behaviours that frequently escalate into physical combat, including biting (Petren et al., 1993; Hoskin, 2011). Larger relative head sizes would likely enhance fighting ability, but may inhibit locomotor performance, especially on vertical surfaces, due to increased energy expenditure against gravity and associated changes in centre of mass away from the vertical substrate (Huey and Hertz, 1982; Vanhooydonck and Van Damme, 1999). Geckos use short bursts of speed to capture prey, escape predators and during territorial male-male conflicts (Hoskin, 2011). Therefore, bite force and sprint speed are both ecologically important activities in this species that may act in opposition. We predicted that, due to their combative nature, male geckos would have larger relative head sizes than females, and this would lead to reductions in locomotor performance. In addition, we expected this trade-off to be further exacerbated when individuals sprint on inclined surfaces because of the greater difficulties of running with a large head up inclines due to an overall increase in body mass (Huey and Hertz, 1982). Alternatively, if we detected no trade-offs between head size and locomotor performance, then we expected to observe compensatory modifications in relative limb lengths that offset any decrements in locomotor function caused by larger heads.

Materials and Methods

Adult male ($n=150$) and female ($n=100$) *Hemidactylus frenatus* were captured from Brisbane, Australia; all geckos had a snout-vent length (SVL) $> 42\text{mm}$ and mass $> 2\text{g}$. Three test groups were captured over a one-year period and maintained in the laboratory for no longer than three months. The total number of geckos and specific test groups used in each experiment and final analysis are provided within the relevant sections below (also see Table 1). In the laboratory, geckos were individually housed in well-ventilated plastic terrariums ($26 \times 17 \times 13 \text{ cm}$) with a newspaper substrate and a $10 \times 5 \text{ cm}$ piece of perforated black plastic piping for a retreat. Terrariums were kept in a controlled temperature room at $24 \pm 1.0^\circ\text{C}$ and a light cycle of 12L: 12D. Heat cord ($9 \text{ m}/90 \text{ W}$) was supplied beneath each terrarium directly below the retreat and was switched on between the hours of 08:00 and 16:00, which allowed individuals to self-regulate body temperature. All geckos were fed a diet of calcium-dusted wood cockroaches and crickets every three days, and water was misted daily. Individuals that had suffered a loss of more than 10 % in body mass, autotomised their tail or suffered other significant health problems during the test period were removed from statistical analyses.

Relationship between bite force and sprint speed in males and females

We recorded the morphometrics, maximum sprint speed and bite force of 46 male and 49 female *H. frenatus* (Test Group 1). The body mass of each gecko was measured, using an electronic balance $\pm 0.01 \text{ g}$ (Sartorius Excellence, GMBH, Göttingen, Germany), at both the start and end of the testing period, with the average of these two measurements used as their measure of body mass. Digital photographs (Casio – EX-FH, China) of the ventral surface of individual geckos were taken to measure seven different body dimensions (Fig. 1): jaw width (at the maximum lateral extent of the temporal jaw-adductor musculature), jaw length (from coronoid-articular jaw joint to tip of snout), body length (from coronoid-articular jaw joint to cloaca) average fore-limb length (humerus and radius), average hind-limb length (femur and fibula), tail width (pre caudal autonomy vertebrae) and tail length (cloaca to tip of tail). All digital photographs of individuals were taken at the end of the test period. As all experiments were less than two months in duration and body mass did not vary by more than 10% for each individual across this period, growth was minimal during the experiments. Images were calibrated and analysed using morphometric software (SigmaScan 5.0, Systat, San Jose, CA,

USA). Principal components analyses (PCA) were used to combine seven morphological variables (SVL was excluded) into an overall measure of body size (PC_{Body}), and jaw width and jaw length were used as measures of head size (PC_{Head}). All PCA measures were calculated with the sexes combined. Overall body size of *Hemidactylus frenatus* is represented by PC_{Body} (first principal component), which accounted for 57% of the variation in the data (Table 2). All loadings were positive, indicating that all seven morphological variables increased together. This species exhibits caudal autotomy; therefore tail length is not as influential as all other morphological variables (only 0.108 variation explained – see Table 2) in PC_{Body} . All geckos that autotomized their tails during testing were excluded from analyses. We also calculated a measure of condition for each individual by calculating residuals of a linear regression of log-transformed body mass by log-transformed SVL.

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Maximum bite force was measured using a custom-built sensor consisting of two metal plates (8 x 25 x 1 mm) separated by a larger third steel metal pivot plate (3 mm thick) with all three plates permanently secured to form one unit. The smaller two plates protruded 12 mm beyond the pivot plate. The top metal plate had a strain gauge (RS Electronics, Sydney, Australia) attached via epoxy resin. The output from the strain gauge was connected to a custom-made Wheatstone bridge linked to a bridge amplifier (AD Instruments, Sydney, Australia) (Wilson et al., 2007). The two protruding plates were covered in three layers of flesh-like tape (Elastoplast, Beiersdorf) to offer a defined biting point and surface. Output from the bridge amplifier was monitored via a data recording system (PowerLab, AD Instruments). A series of weights ranging from 100 to 1000 g were suspended from the bite point to calibrate the output. Calibrations reflected the force applied during bites to the biting point. The strain gauge was calibrated daily prior to use so that the voltage output from the bridge amplifier could be converted to force (N).

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Geckos were briefly induced to bite forcefully on the ‘bite point’ of the sensor by placing the bite plates between the gecko’s open jaws. If a maximum bite was not attained or biting did not occur on the “bite point”, geckos were rested and a second attempt was made after 10 minutes. A minimum of five maximum bites per individual were recorded in each of the two separate test periods, with two weeks between each test period (repeatability of maximum bite forces was calculated using the single best performance for each individual from each

201 test period; Pearson's product-moment correlation ($r=0.81$, $d.f.=200$, $p<0.001$). The
202 maximum of the 10 bites was used as the measure of an individual's bite force (N). Prior to
203 measuring maximum bite force, all geckos were equilibrated to $24 \pm 1^{\circ}\text{C}$ in a controlled
204 temperature room for a minimum of 90 min.

205
206 Maximal sprint speed was measured using a custom-built perspex runway (100 x 7 x 10 cm)
207 fitted with four infrared LED light gates. Light gates were positioned towards the middle of
208 the runway at 10 cm intervals. Output from the LED light gates was monitored via a four-
209 channel data recording system (PowerLab, AD Instruments, Sydney, Australia). Sprints were
210 elicited by placing individuals in the start position of the runway and chasing them to the
211 opposite end using a foam brush the width of the runway. Geckos were made to run along the
212 runway four times during each test period. Sprint speed was then calculated for each of the
213 three 10 cm distances between consecutive light gates for all four runs during each testing
214 period (i.e. 12 measures of sprint speed per testing period) (Hertz et al., 1982; Angilletta et
215 al., 2002; Adolph and Pickering, 2008). All geckos were then re-tested in the same manner
216 after a two week rest period (repeatability of maximum sprint speeds was calculated using the
217 single best performance for each individual from each test period repeatability between two
218 test periods; Pearson's product-moment correlation ($r=0.13$, $d.f.=300$, $p=0.023$). From the 24
219 time splits recorded per individual, the fastest was then used as their measure of maximum
220 sprint speed (cm sec^{-1}). Prior to measuring maximum sprint speed, all geckos were
221 equilibrated to $24 \pm 1^{\circ}\text{C}$ in a controlled temperature room for a minimum of 90 min.

222
223 **Influence of incline angle on sprint speed**

224 We examined the influence of incline angle on the sprint speed of 44 male and 47 female *H.*
225 *frenatus* (Test Group 2). We quantified sprint performance of each individual at 0° and 60° by
226 adjusting the incline angle of the custom-built runway. Individual bite force and morphology
227 was also quantified. These two angles were chosen, excluding a 90° angle, as geckos would
228 not sprint consistently on vertical incline on the Perspex substrate. A 60° incline was the
229 maximum angle on which sprint speed remained significantly repeatable. Sprint speed was
230 measured using methods identical to those outlined above and the order for testing
231 performance at each incline angle was randomised for each individual. The proportional

232 decrease in sprint speed was calculated by sprint speed at 60° divided by sprint speed at 0°
 233 (60°/0°). The morphology of each individual gecko and bite force were also quantified (as
 234 above) to determine the influence of overall head size and biting capacity on the relative
 235 decrease in sprint speed with an increase in incline.

236

237 Determinants of dominance

238 We recorded the morphometrics, bite performance, sprint speed and dominance of individual
 239 male geckos (from Test Group 1), using staged dyadic bouts of 25 focal males and 25 male
 240 opponents. Opponents were divided into three size classes (small, medium and large) by
 241 body mass. Each focal male was competed against a randomly selected opponent male, one
 242 from each of the size classes in random order. Size classes were used as we were interested in
 243 all factors, and interactions, that affect the outcome of male fights and it is also well
 244 documented that body size can affected dominance (Perry et al., 2004). All males (focal and
 245 opponent) were competed a total of three times, with individuals never encountering the same
 246 male twice. All 75 bouts were conducted within a darkened, temperature-controlled room set
 247 at $24 \pm 1^{\circ}\text{C}$. Geckos were equilibrated to 24°C for 90 min whilst maintained in their
 248 individual terrariums before each bout and received a 48 hr rest period between bouts.

249

250 To start each bout, focal and opponent geckos were simultaneously introduced to opposite
 251 sides of a 60 cm x 30 cm x 30 cm sealed glass terrarium. A limited resource (heat point in the
 252 tank) was provided to facilitate interactions between males. Each focal gecko was marked
 253 with three small dots of neutral white non-toxic acrylic paint for identification - on the dorsal
 254 side of the head and torso and the tip of the tail (Lailvaux et al. 2004; Jenssen, Decourcy &
 255 Congdon 2005). To allow all observations to be conducted in darkness, thus excluding
 256 observer effects and representing nocturnal habitat, each bout was filmed using a Sony
 257 handheld camera (Sony DCR-HC52E, Japan) on night-shot setting using infrared lights. Each
 258 bout was recorded for 30 minutes from the time of initial introduction to the arena. This
 259 period allowed sufficient time for one of the individuals to attain dominance, as geckos
 260 generally interacted immediately.

We scored each male's dominance status using a range of observed behaviours, with the scoring system modified from studies of dominance in other lizard species (Garland et al., 1990; Lailvaux et al., 2004; Perry et al., 2004; Huyghe et al., 2005; Lailvaux and Irschick, 2007). As the dominance behaviour of *H. frenatus* has not previously been studied, we used pilot studies to rate each interactive behaviour; with more frequent and less aggressive or submissive behaviours receiving lower scores in comparison to less frequent, more costly and territorial behaviours. Both focal and opponent males were scored on a scale that reflected their aggressiveness (i.e. bite [3 points], nudge [2 pts], body arch [2 pts], chase [2 pts], tail wag [1 pt] and access to limited resource [0.5 pts]). Submissive behaviours received negative points depending on the level of sub-ordination (i.e.: retreat/avoidance [-3 pts] and chased away [-2 pts]). Extra points were awarded or deducted for winning or losing a direct physical fight (1/-1 pts, respectively), with no result yielding zero points. Dominance rankings were based on an individual focal male's overall score across all three bouts (focal male score minus that of their opponents). Male geckos that lost more than 10% of body mass and/or autotomised their tale, at any point during the test period, were excluded from analyses (Focal $n=2$, Opponent $n=2$).

Determinants of prey-capture performance

We recorded the morphometrics, bite performance, sprint speed and prey capture performance of 50 individual male geckos (Test Group 3). To quantify prey capture ability we assessed each individual's capacity (total time taken in seconds; where 0 seconds is the fastest prey capturing ability and 600 seconds is the slowest) to capture live crickets (*Acheta domesticus*) during staged feeding trials (modified from Verwaijen et al., 2002). All feeding trials were conducted within a controlled temperature room set at $24 \pm 1^\circ\text{C}$ and within the geckos' permanent terrarium so as to reduce stress. Each gecko was fasted for three days prior to testing and all substrate, excess food and waste was removed from the terrarium. To exclude observer effects, each trial was filmed using a Sony handheld camera and recorded for 10 min from the time of the initial introduction of the prey (130 ± 20 mg). If a gecko had not captured the prey within this time they received the total time of 10 min (600 sec), the cricket was removed and the trial was ended. One prey item was introduced into each terrarium each day for five consecutive days. Maximum prey capture was the fastest time (0

292 sec – 600 sec) of the five trials for individual geckos. If the gecko did not capture any prey
 293 during these five trials they were removed from the analysis ($n=5$) with the assumption that
 294 they were unmotivated or too stressed. Time to capture prey was repeatable with no
 295 significant difference between each trial (one-way ANOVA with Tukeys HSD *post hoc*
 296 comparison: $F_{4,245}=0.80$, $p=0.53$).

298 **Statistical analysis**

299 Statistical analyses were performed using R (version 2.11.1) unless otherwise specified.
 300 Significance was taken at the level of $p<0.05$. Both Pearson's product-moment correlations
 301 and multiple linear regressions with model simplification were used to establish whether
 302 morphology and/or sex affected performance. We calculated size-corrected measures of
 303 morphological traits (head size, fore and hind limb lengths, tail width and tail length) by
 304 generating residual values of the particular trait regressed on SVL.

306 A multiple linear regression was used to investigate if there was a functional trade-off
 307 between bite force and sprint speed. We examined the relationship between relative head size
 308 and bite force with the proportional decrease in sprint speed up an incline using Pearson's
 309 product-moment correlation for each sex separately. To assess if compensation was masking
 310 any potential trade-offs, we investigated the relationships between relative head size and
 311 other morphological variables that could affect sprint speed. Males and females were
 312 analysed separately using a Pearson's product-moment correlation. Furthermore, to
 313 investigate if hind limb length is a potential compensatory mechanism we used residuals of
 314 relative head size on relative hind limb length. This measure of hind limb length corrected for
 315 head size was then used to identify if compensation resulted in increased locomotor
 316 performance (sprint speed), off-setting costs of increased head size via a Pearson's product-
 317 moment correlation, again with sexes analysed separately.

318 Path analyses were used to describe the relationship between morphological and performance
 319 traits with both dominance and prey capture abilities (AMOS 5.0, SPSS Inc., Chicago, IL,
 320 USA). The model design is modified from Oufiero and Garland (2007), to assess body mass
 321 (as these would co-vary with sexually selected traits and may influence performance
 322 capacity), sexually selected traits, compensatory traits, performance and the effects on fitness

323 (see Fig 1. in Oufiero and Garland, 2007). The morphological measures of body mass (g),
 324 condition (as described above), head size (PC_{Head}) and hind limb length (mm) were used in
 325 combination with the two performance traits of bite force (N) and sprint speed (cm sec^{-1}). Ten
 326 models describing the relationship between these variables with either dominance or prey
 327 capture were tested. The most complex model included all interactions (Model A) while
 328 simplified versions contained varying combinations of the variables (Models B – J; see Fig.
 329 A1 in Appendix). All ten models for dominance and prey capture were ranked by calculating
 330 second-order Akaike information criterion (AIC_C):

$$331 \quad AIC_C = \chi^2 + 2K + (2K(K+1))/(N-K-1)$$

332 where χ^2 = Chi-square goodness of fit, K = number of estimated parameters and N = sample
 333 size (Angilletta, Oufiero & Leache 2006). AIC_C values were used to assess which model
 334 explained the most variation in dominance and prey capture in relation to model complexity
 335 by Akaike weights (w_i).

336

Results

Relationship between bite force and sprint speed in males and females

Male *H. frenatus* were on average 20% larger than females (mean male mass = 3.61 ± 0.10 g; $PC_{\text{Body}} = 1.08 \pm 0.29$ and mean female mass 3.01 ± 0.07 g; $PC_{\text{Body}} = -1.00 \pm 0.18$). Head size (PC_{Head}) scaled positively with overall body size (PC_{Body}) for both sexes ($r = 0.94$, d.f. = 96, $p < 0.001$), with males possessing larger overall head sizes than females (mean male $PC_{\text{Head}} = 0.61 \pm 0.2$ and female mean $PC_{\text{Head}} = -0.70 \pm 0.13$).

Bite force was significantly positively associated with body size ($R^2 = 0.353$, $F_{1,96} = 52.45$, $p < 0.001$; Fig. 2A) and head size ($R^2 = 0.306$, $F_{1,96} = 42.44$, $p < 0.001$). In both cases there was no significant effect of sex on bite force (body size: $t = 0.467$, $p = 0.642$ and head size: $t = 0.797$, $p = 0.428$), nor were there any significant interactions between sex, bite force and size (body size: $t = 0.015$, $p = 0.988$ and head size: $t = -0.107$, $p = 0.915$). Overall males had stronger bite force than females, however there was no difference once corrected for body size (PC_{Body}) ($R^2 = 0.006$, $F_{1,96} = 0.61$, $p = 0.437$). Sprint speed was significantly associated with body mass ($t = 2.53$, $p = 0.013$) and sex ($t = 3.99$, $p < 0.001$), though in opposite directions for males and females. Male sprint speed decreased with increasing body mass, whereas female sprint speed increased with increasing in body mass ($R^2 = 0.14$, $F_{3,94} = 6.03$, $p < 0.00$; Fig. 2B). A similar trend for the effects of body size (PC_{Body}) and sex on sprint speed were observed, however it was not statistically significant (body size: $t = 1.72$, $p = 0.097$, sex: $t = 1.00$, $p = 0.319$, body size*sex: $t = -1.74$, $p = 0.085$).

The relationship between bite force and sprint speed was significantly affected by sex ($R^2 = 0.106$, $F_{3,94} = 3.72$, $p = 0.014$), with males displaying a negative relationship between these two traits. Bite force was negatively correlated with sprint speed for male *H. frenatus* ($r = -0.315$, d.f. = 46, $p = 0.029$; Fig. 3A), however females showed no significant relationship between bite force and sprint speed ($r = 0.194$, d.f. = 48, $p = 0.178$; Fig. 3B).

Determinants of dominance and prey capture performance

Among the ten path models, Model I best described the relationships among morphology, performance and dominance ($\chi^2 = 26.5$, df = 7, $K = 20$, $AIC_C = 50.7$, $w_i = 0.35$; Fig. 4A)(see

Table A1 in Appendix). Within this model, dominance was significantly positively associated with bite force ($p=0.004$), while sprint speed had a negative relationship ($p=0.136$). Hind limb length had no significant effect on either bite force ($p=0.887$) or sprint speed ($p=0.983$), and was not related to body mass ($p=0.408$). However, head size was significantly positively associated with both body mass ($p<0.001$) and bite force ($p=0.001$). Overall male body mass and head size affected dominance via their influence on bite force but not sprint speed. A similar trend was seen in the second most likely model, Model G ($\chi^2 = 17.9$, $df = 6$, $K = 21$, $AIC_C = 51.2$, $w_i = 0.256$), with the addition of a significantly positive covariance between head size and hind limb length ($p=0.016$).

The relationships among morphology, performance and prey capture ability were more than 60% likely to be best described by Model G ($\chi^2 = 5.2$, $df = 6$, $K = 21$, $AIC_C = 38.6$, $w_i = 0.60$; Fig. 4B) (see Table A2 in Appendix). Based on this model, bite force ($p=0.002$), but not sprint speed ($p=0.603$) was negatively correlated with an individual's prey capture time. Thus geckos with stronger bites captured prey faster than those with weaker bites. For prey capture performance, body mass was significantly positively correlated with head size ($p=0.002$) as well as hind limb length ($p=0.069$); head size and hind limb length were also positively correlated ($p=0.004$). In this model individuals with larger heads also had stronger bites and faster sprint speeds ($p=0.106$), but hind limb length was not related to either performance traits (bite force; $p=0.501$ and sprint speed; $p=0.420$).

Influence of incline angle on sprint speed

A geckos sprint speed at 60° incline as a proportion of their speed at the horizontal was not affected by body size (PC_{Body}) ($t=-1.806$, $p=0.074$), but sex did affect this proportion ($t=2.26$, $p=0.026$). Larger males had slower sprint speeds at a 60° incline as a proportion of their speed at the horizontal ($R^2=0.054$, $F_{2,92}=2.64$, $p=0.076$). Bite force ($t=-2.01$, $p=0.047$) and sex ($t=2.40$, $p=0.018$) independently affected the proportional decrease in sprint speed, with increases in the bite force of males associated with lower sprint speeds at a 60° incline relative to their speed at the horizontal ($R^2=0.062$, $F_{2,92}=3.04$, $p=0.050$). As male head size (PC_{Head}) increased, we also observed a decrease in sprint speed between the two inclines ($r=-0.329$, $d.f.=44$, $p=0.026$; Fig. 5A); however this relationship was absent in females ($r=0.006$, $d.f.=47$, $p=0.969$; Fig. 5B).

Compensatory traits

We found no significant relationship between relative head size and any of the relative morphological variables for male *H. frenatus* (relative fore limb length: $r=-0.127$, d.f.=44, $p=0.401$; relative hind limb length (Fig. 6A): $r=0.091$ d.f.=44, $p=0.548$; relative tail width: $r=0.070$, d.f.=44, $p=0.643$ and relative tail length: $r=-0.045$, d.f.=44, $p=0.758$). In females, however, relative head size was significantly positively correlated with both relative hind limb length ($r=0.307$, d.f.=47, $p=0.032$; Fig. 6B) and relative tail width ($r=0.420$, d.f.=47, $p=0.003$); that is, females which had proportionally longer hind limbs and wider tails also had relatively larger heads. In contrast, relative fore limb length ($r=0.267$, d.f.=47, $p=0.063$) and relative tail length ($r=0.111$, d.f.=47, $p=0.449$) were not significantly associated with relative head size for females. For both sexes, sprint speeds were not affected by relative hind limb length, corrected for relative head size, at either 0° incline (males: $r=0.185$, d.f.=44, $p=0.218$ and females: $r=-0.190$, d.f.=47, $p=0.191$) or 60° inclines (males: $r=-0.075$, d.f.=44, $p=0.621$ and females: $r=-0.071$, d.f.=47, $p=0.623$).

Discussion

Selection rarely acts on a single trait in isolation, but rather on a combination of traits (Calsbeek and Irschick, 2007). In our study, we investigated how differing selection pressures on performance traits may result in a compromised phenotype (trade-off); specifically we evaluated trade-offs between traits linked to dominance (bite force) and prey capture or predator avoidance (sprint speed). We also investigated whether any compensatory mechanisms offset some of the associated reductions in performance. We found support for our prediction that a trade-off exists between those traits associated with bite force and those associated with locomotor performance in the Asian house gecko (*Hemidactylus frenatus*). Males that had a greater biting capacity due to larger head sizes suffered reduced sprint performances, and this trade-off was further exacerbated when sprinting on an incline. Females, however, showed no evidence of this trade-off on either flat or inclined surfaces. The sex specificity of this trade-off suggests that males and females may differ in their optimal strategies for dealing with the conflicting requirements of bite force and sprint speed. Females with larger heads also had longer hind limbs, indicating the possible presence of a compensatory mechanism to reduce the locomotor costs associated with head size.

The magnitude of sexual dimorphism varies greatly among species and may reflect the divergent selective pressures operating on each sex, and among different species (Herrel et al., 2012). We expected that the high level of territoriality and combat exhibited by male *H. frenatus* would result in larger relative head sizes for males. However, we did not find this to be the case. Males were only larger than females in overall body size but not relative head size. Larger body sizes in the males of other lizard species are associated with increased bite performances and success in territorial combats (e.g. (Anderson and Vitt, 1990; Herrel et al., 1996; Herrel et al., 1999; Verwaijen et al., 2002; Lailvaux et al., 2004; Huyghe et al., 2005). Our path analyses of dominance hierarchies support this idea, and demonstrate that an increase in body size leads to greater male-male combat success; bite force was the most important performance trait, of the traits measured, underlying male success in territorial combats. Recent studies have found similar correlations between bite force and dominance in other lizard species (Lailvaux et al., 2004; Huyghe et al., 2005). For example, Huyghe et al. 2005 found that in *Gallotia galloti* bite force was the most important predictor of the outcome for male-male combat. These findings suggest there may be direct sexual selection for

445 increased bite force in both male *H. frenatus* and *G. galloti*, which provides an advantage
 446 during male-male combat and possibly mating with females, indirectly driving the increase in
 447 head size or in this case for *H. frenatus* overall body size (Lappin et al., 2006; Husak and
 448 Swallow, 2011).

449
 450 The functional trade-off we observed between bite force and sprint speed performance in
 451 male *H. frenatus* suggests the presence of conflicting demands on male fighting ability and
 452 locomotor performance (Lopez and Martin, 2002); the locomotor performance of dominant,
 453 larger-headed males was even poorer on inclines. We believe these results demonstrate how
 454 habitat selection can mediate the expression of functional trade-offs: the narrow crevices and
 455 compact retreat sites utilised by *H. frenatus* for anti-predatory behaviour may explain why
 456 males do not exhibit increased relative head sizes compared to females (Lappin et al., 2006;
 457 Hoskin, 2011). Other lizard species inhabiting vertical surfaces also tend to have a reduced
 458 head to body ratio which allows the centre of mass to be kept closer to the substrate, reducing
 459 the tendency to topple backwards (Vanhooydonck and Van Damme, 1999; Verwaijen et al.,
 460 2002). Therefore to retain the ability for a greater biting capacity, whilst remaining within the
 461 constraints of the chosen habitat, males may increase overall body sizes but not relative head
 462 sizes. The absence of sexual dimorphism in relative head size in *H. frenatus* however, may
 463 also be due to the importance of biting capacity for both males and females (Herrel et al.,
 464 1998; Verwaijen et al., 2002; Vincent and Herrel, 2007). Although not investigated in this
 465 study, increased bite force and therefore head size in female *H. frenatus* may also be under
 466 natural selection to increase prey capturing ability, resulting in a bigger head, as is the case
 467 for male *H. frenatus*. Even though prey capture is likely to be more complex than our model
 468 assumes, previous studies also suggests that both bite force and head morphology are highly
 469 relevant for feeding capacity and ability to capture food and are therefore under natural
 470 selection (Herrel et al., 1998; Verwaijen et al., 2002; Verwaijen and Van Damme, 2007;
 471 Vincent and Herrel, 2007; Kaliontzopoulou et al., 2012).

472
 473 In contrast with our study, several previous studies have found greater locomotor
 474 performance to be positively associated with social dominance (Garland et al., 1990; Hews,
 475 1990; Robson and Miles, 2000; Lailvaux et al., 2004; Perry et al., 2004; Husak et al., 2006;
 476 Peterson and Husak, 2006; Hall et al., 2010). On the other hand a study by Huyghe et al.,

(2005), found no correlation between locomotor performance but rather increased bite force capacity and dominance (Huyghe et al., 2005). The direct functional importance of locomotor performance to dominance is difficult to determine but is may not be directly related to individual combat success but rather may be a more general indicator of overall male quality (e.g. (Lailvaux et al., 2004; Hall et al., 2010). Lopez and Martin (2002), found a trade-off between head size and locomotor performance for the lizard *Lacerta monticola*; unlike male *H. frenatus*, however, it appears that this trade-off was attributable to reduced energy allocation during breeding season and not a biomechanical constraint (Lopez and Martin, 2002). However, bite force of *L. monticola* in this study was not assessed. These contrasting results may be a result of differing social and sexual behaviours and fighting strategy, with selection for different performance variables. However intraspecific variation in things such as foraging ability, predation intensity and habitat selection and the role they play on how sexually selected traits may evolve could also be of great importance (Petren and Case, 1998; Huyghe et al., 2005).

We found that female *H. frenatus* with relatively larger heads also had relatively longer hind limbs. This morphological correlation was the likely mechanism for the absence of a trade-off between bite force and sprint speed within females. In contrast, male *H. frenatus* showed no such modification in the limb length, and males that had larger heads may have suffered reduced locomotor performance as a consequence. However, these assessments are merely speculative; though previous studies report limb length as an important determinant of spring speed (Vanhooeydonck et al., 2001; Husak, 2006), we did not find a correlation between relative hind limb length (corrected for head size) and sprint speed in geckos. This result however may be due to the low repeatability, or noise within measures of sprint speed of individuals. Male *H. frenatus* however did not provide evidence for a compensatory increase in limb length to mediate any reduction in locomotor performance. This may be due to males having varying energy allocation requirements to achieve and maintain a certain level of dominance, such as increased body size and production of testosterone (Sinervo et al., 2000; Husak et al., 2007). However, it seems that there are alternate costs for possessing larger heads for male and female *H. frenatus*. Males pay the direct costs on locomotor performance while females pay an energetic cost through investment in longer limbs.

508 Taken together, our results clearly suggest that performance trade-offs may limit the
509 exaggeration of sexually selected traits, but such costs have the potential to be mitigated by
510 compensatory morphological changes. For *H. frenatus*, this suggests there is a greater
511 selection on traits associated with dominance (i.e. bite force) for males and survival (i.e.
512 sprint speed) for females.

513

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516 We also thank two anonymous reviewers, J. Husak, D. Booth, C. White and A. Niehaus for
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518 of Queensland's Animal Ethics Committee (AEC approval number - SBS/319/09).

519

520 **Figure Headings:**

521 **Figure 1:** Photograph of the ventral surface of a male gecko Asian house gecko
522 (*Hemidactylus frenatus*). Morphological variables measured: jaw width (at the maximum
523 lateral extent of the temporal jaw-adductor musculature), jaw length (from coronoid-articular
524 jaw joint to tip of snout), body length (from coronoid-articular jaw joint to cloaca) average
525 fore-limb length (humerus and radius), average hind-limb length (femur and fibula), tail
526 width (pre caudal autonomy vertebrae) and tail length (cloaca opening to tip of tail). Snout-
527 vent length (SVL – sum of jaw length and body length) is also shown on figure as it was used
528 in various analyses. All variables were combined for each individual via principal component
529 analyses to gain an overall measure of body size (PC_{Body} - seven variables – excluding SVL)
530 and head size (PC_{Head} - jaw width and jaw length).

531 **Figure 2:** The relationship between body mass (g) and **A:** bite force (N) and **B:** sprint speed
532 (cm sec⁻¹). Males (n=47) are represented by full circles and females (n=49) by empty circles.
533 There was a significant positive effect of mass on bite force but not of sex or any interaction
534 between the two predictors ($R^2=0.353$, $F_{1,96}=52.45$, $p<0.001$). Sex, mass and an interaction
535 of predictors had a significant effect on sprint speed ($R^2=0.14$, $F_{3,94}=6.03$, $p<0.001$).

536 **Figure 3:** The relationship between bite force (N) and sprint speed (cm sec⁻¹) for **A:** male and
537 **B:** female *Hemidactylus frenatus*. There was a significant negative correlation (trade-off)
538 between bite force and sprint speed for males ($r=-0.315$, d.f.=46, $p=0.029$) but not for females
539 ($r=0.194$, d.f.=48, $p=0.178$) analysed separately using a Pearson's product-moment
540 correlation.

541 **Figure 4:** The best predictive models described by path analyses and selected by AICc which
542 describe the relationships among morphological traits body mass (g), head size and hind limb
543 length (mm), performance traits (bite force (N) and sprint speed (cm sec⁻¹) and **A:** dominance
544 – Model I (see Fig. A1-I) which explains 33% of variation in dominance and **B:** prey capture
545 – Model G (see Fig. A1-G) explaining 22% of variation in time to capture prey for male
546 *Hemidactylus frenatus*. Standardized coefficients are provided for each path ($^{\circ}p<0.1$, * = $p <$
547 0.05 , ** = $p < 0.01$ and *** $p<0.001$).

548 **Figure 5:** The relationship between head size (PC_{Head}) and sprint speed of males at a 60°
549 incline as a proportion of sprint speed at no incline (0°) for **A:** male and **B:** female
550 *Hemidactylus frenatus*. There was a significant negative correlation (trade-off) for males
551 ($r=-0.329$, d.f.=44, $p=0.026$) but no significant correlation for females ($r=0.006$, d.f.= 47,
552 $p=0.969$).

553 **Figure 6:** Relationship between relative head size (residual PC_{Head} by SVL) and relative hind
554 limb length (residual hind limb by SVL) for **A:** male and **B:** female *Hemidactylus frenatus*.
555 There was a significant positive correlation for females ($r=3.07$, d.f.=47, $p=0.032$) but no
556 significant correlation for males ($r=0.091$ d.f.=44, $p=0.548$).

557

558 **Appendix**

559 **Figure A1:** The ten path models depicting the relationships among morphological and
560 performance traits with dominance for male *Hemidactylus frenatus*. The same path models
561 were used for examining the relationships among morphology, performance and prey capture
562 (*substituting prey capture measurements for dominance*).

563

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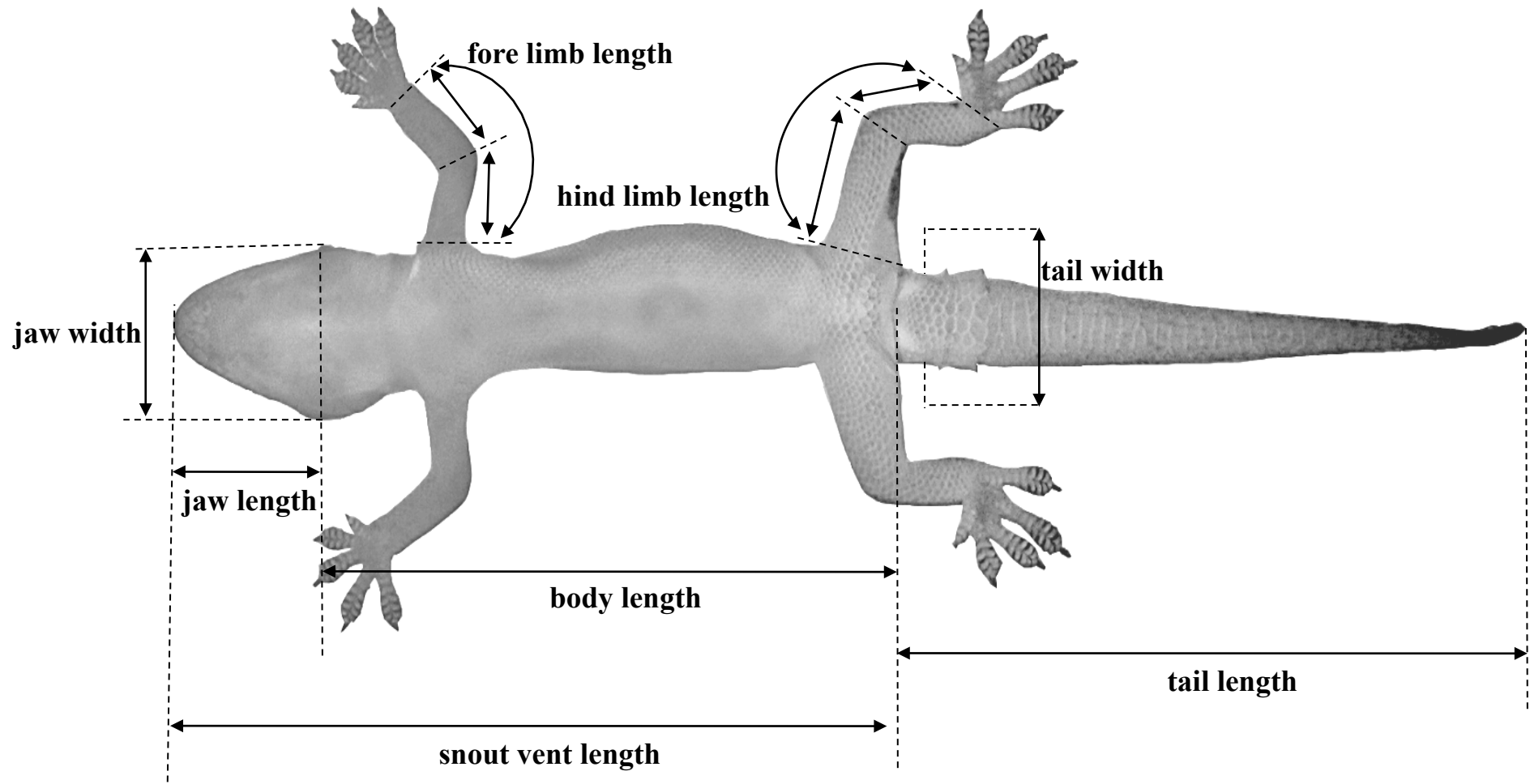
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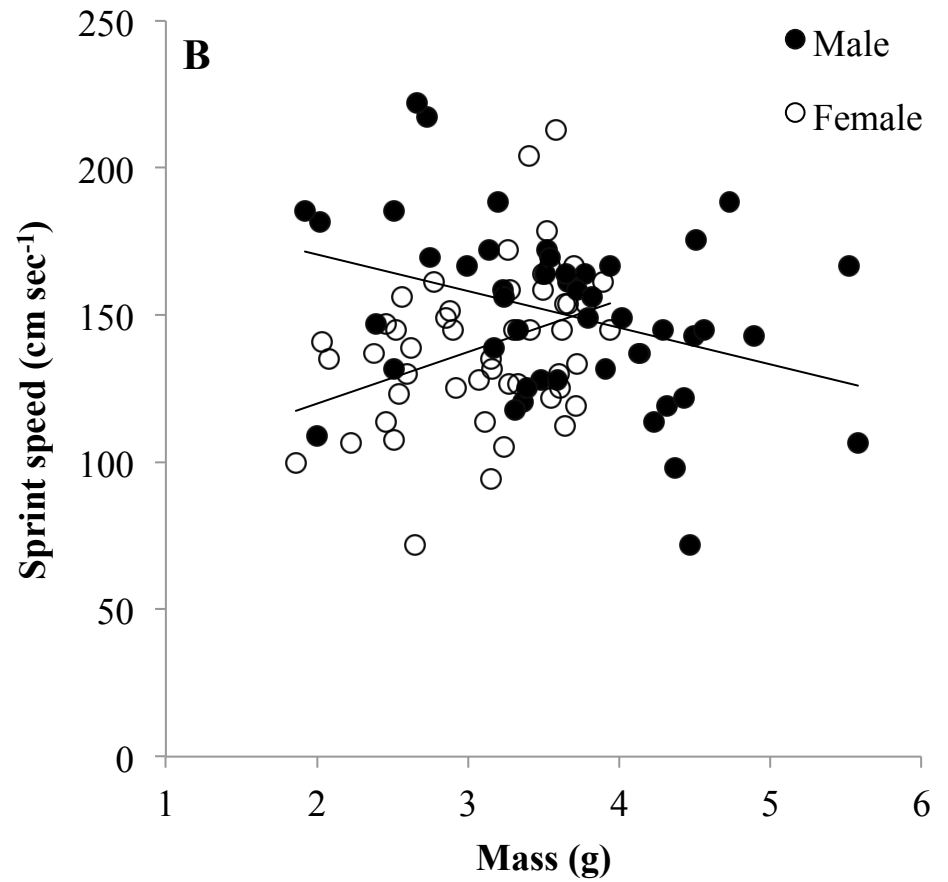
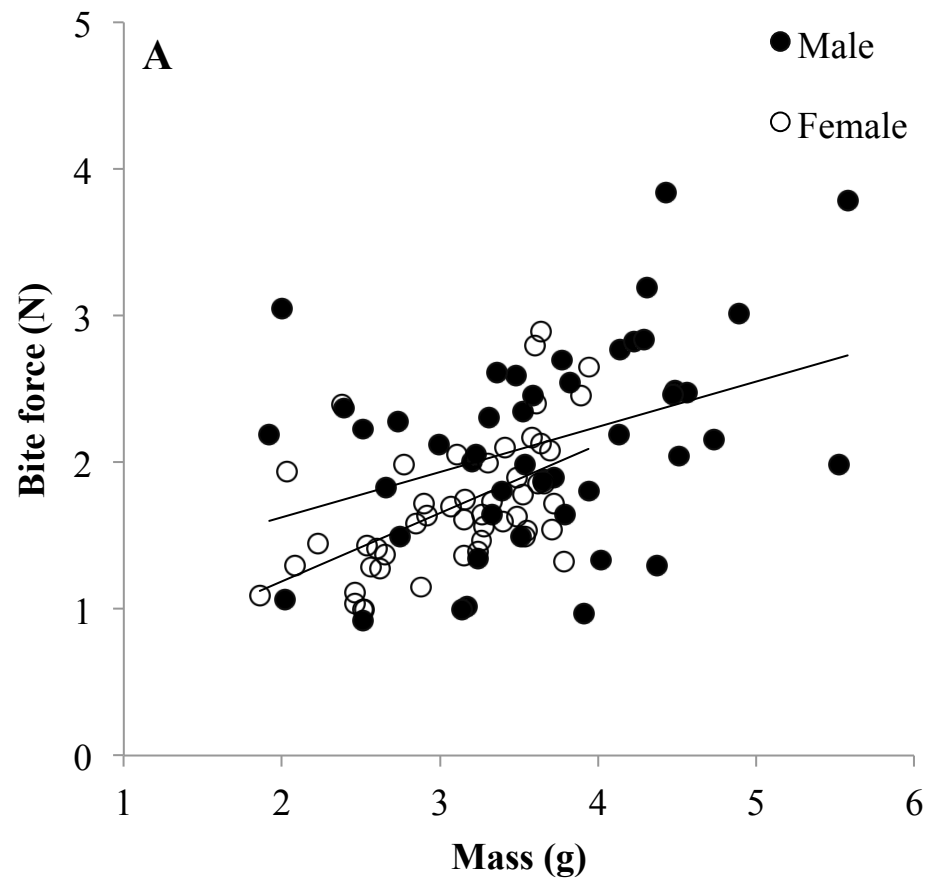
Table 1: A summary of all details for each of the three test groups used in the study: total number of males (*n*) and females (*n*), what measurements were obtained for each test group and how these related to the associated aims within this study provided. For final numbers of geckos used in analyses refer to specific aim sections within methods.

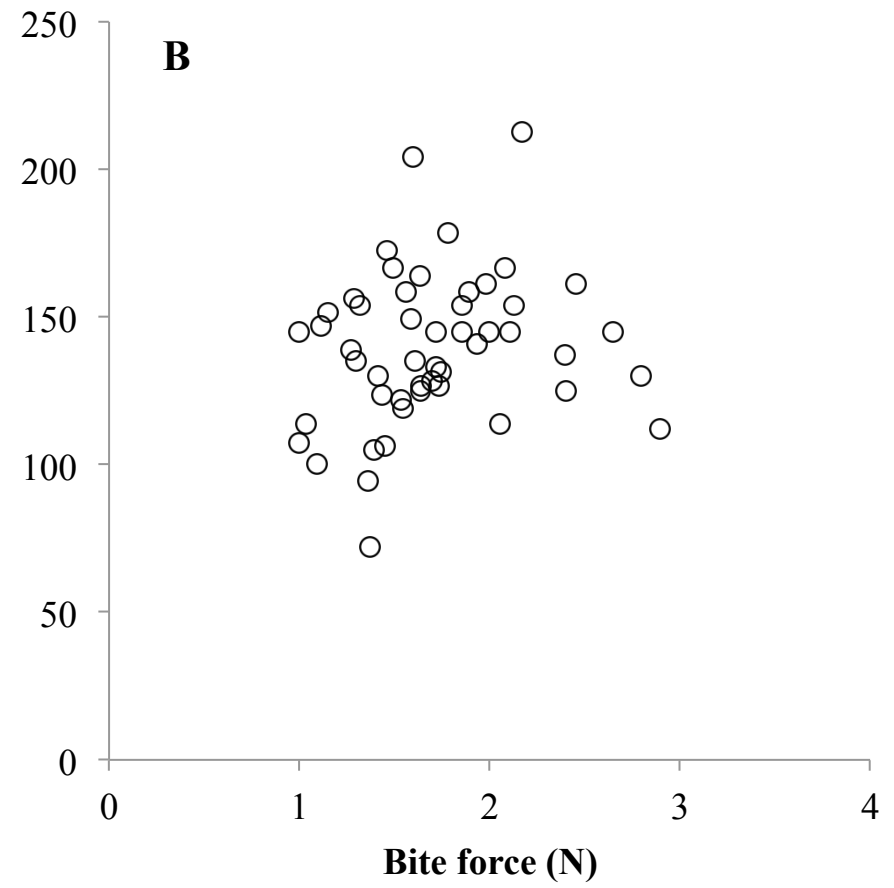
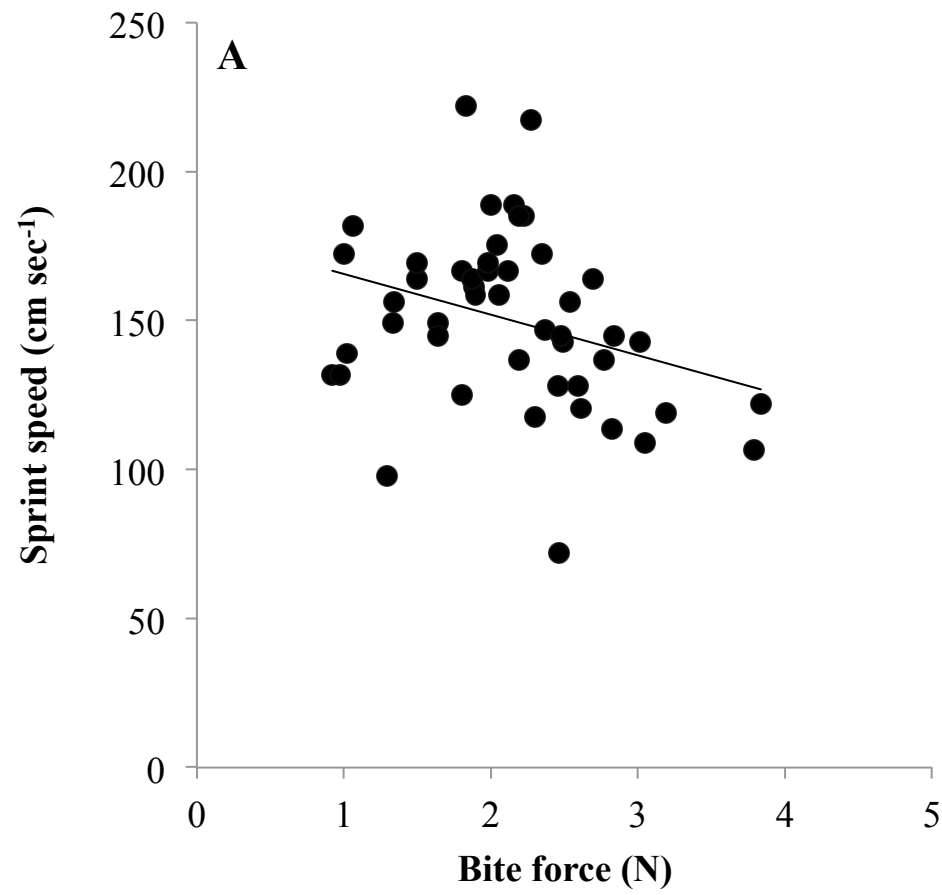
Test Group	Male <i>n</i>	Female <i>n</i>	Morphology	Bite force	Sprint speed	Aim
1	50	50	Yes	Yes	Yes	Relationship between bite force and sprint speed in males and females
			Yes	Yes	Yes	Determinants of dominance
2	50	50	Yes	Yes	Yes	Influence of incline angle on sprint speed
3	50	Nil	Yes	Yes	Yes	Determinants of prey-capture performance

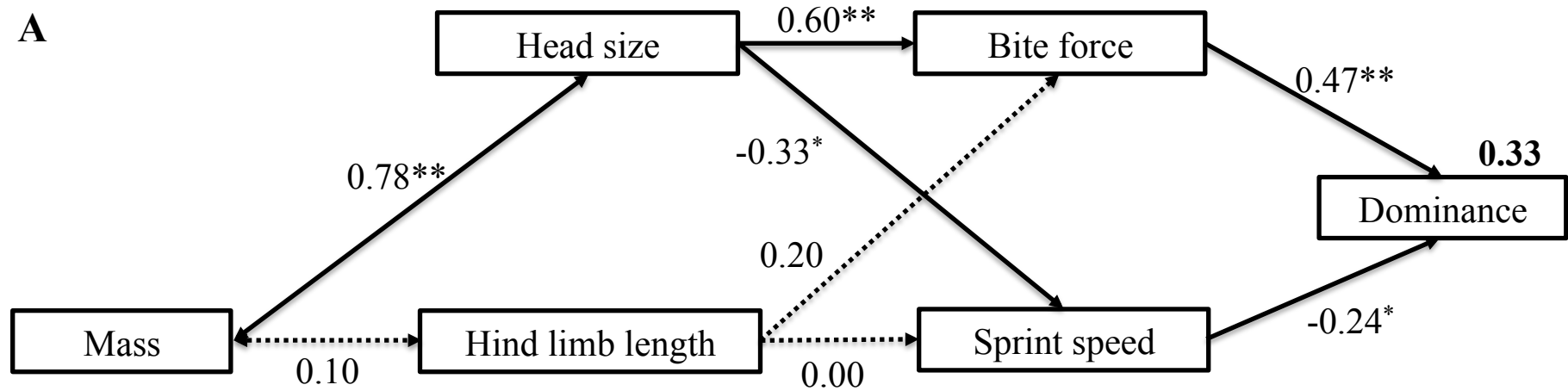
727 **Table 2:** A summary of the principal component analysis (PCA) for body dimensions of
 728 *Hemidactylus frenatus* (PCA includes both sexes from Test Group 1). Values represent the
 729 relative contributions of each of the seven morphological variables (see Fig. 1) towards each
 730 of the components. Missing values indicate loadings less than 0.1. PC_{Body} explains 57% of
 731 variation and corresponds to overall body size with all variables loading positively.

Morphological variables	PC _{Body}	PC 2	PC 3	PC 4
Jaw width	0.455	0.234		
Jaw length	0.429	0.133		
Body length	0.453	0.175		-0.317
Tail width	0.395	0.254	0.368	0.521
Tail length	0.108	-0.645	0.722	-0.200
Fore limb average	0.280	-0.582	-0.422	0.588
Hind limb average	0.397	-0.279	-0.307	-0.489
<i>Proportion of variance</i>	57%	16%	13%	4%







A**B**