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Directional selection on body size but no apparent survival cost to being large in wild New Zealand giraffe weevils

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When an individual's reproductive success relies on winning fights to secure mating opportunities, bearing larger weapons is advantageous. However, sexual selection can be extremely complex, and over an animal's life the opportunity to mate is influenced by numerous factors. We studied a wild population of giraffe weevils (*Lasiorhynchus barbicornis*) that exhibit enormous intra and intersexual size variation. Males bear an elongated rostrum used as a weapon in fights for mating opportunities. However, small males also employ sneaking behavior as an alternative reproductive tactic. We investigated sexual selection on size by tracking individual males and females daily over two 30-day periods to measure long-term mating success. We also assessed how survival and recapture probabilities vary with sex and size to determine whether there might be a survival cost associated with size. We found evidence for directional selection on size through higher mating success, but no apparent survival trade-off. Instead, larger individuals mate more often and have a higher survival probability, suggesting an accumulation of benefits to bigger individuals. Furthermore, we found evidence of size assortative mating where males appear to selectively mate with bigger females. Larger and more competitive males secure matings with larger females more frequently than smaller males, which may further increase their fitness.

KEY WORDS: **Alternative reproductive tactics, brentidae, exaggerated traits, mark-recapture, sexual selection, size-assortative mating.**

Sexual selection drives the evolution of exaggerated traits such as elaborate weapons and ornaments across a diversity of animals (Zahavi 1975; Andersson 1994; Andersson and Simmons 2006; Emlen 2008). When variation in mating success corresponds with physical attributes, including size or the possession of exaggerated traits, selection on these traits is typically strong (Madsen et al. 1993; Panhuis and Wilkinson 1999; Kelly 2005, 2006; Emlen 2008; Simmons and García-González 2008; O'Brien et al. 2017). For example, male tree wētā (*Hemideima crassidens*) with larger mandibles, which are used as weapons during fights, are more successful at competing for and accessing female harems therefore increasing their mating opportunities (Kelly 2005, 2006). Variation in fitness between individuals can drive selection on body size and exaggerated traits in three main directions. It can be either disruptive, as in the case of alternative reproductive tactics (Moczek and Emlen 2000), stabilizing, where average individuals have higher fitness (Thompson and Fincke 2002), or (most commonly) directional, such as in *Drosophila melanogaster*, where males with more elongated wings are more successful at courting and acquiring a mate (Menezes et al. 2013). Overall, studies of mating success improve our understanding of what drives and maintains variation in reproductive success and exaggerated traits, and how these selection pathways might vary (Partridge and Farquhar 1983; Banks and Thompson 1985; Koenig and Albano 1987; Andersson 1994).

Although bearing larger weapons or ornaments can directly increase reproductive success, size can also pose a significant cost through natural selection pressures, including viability selection and survival costs (Partridge and Farquhar 1983; Banks and Thompson 1985; Gwynne et al. 2007; Wheeler et al. 2012; Ercit and Gwynne 2015; Gwynne et al. 2015; Tammaru et al. 2018). For example, wider heads and smaller legs in male tree crickets (*Oecanthus nigricornis*) are more attractive to females and increase mating success, but negatively impact their ability to avoid predators, with narrower heads and longer legs conferring higher survival (Ercit and Gwynne 2015). Similarly, in the dance fly (*Rhamphomyia longicauda*) females rely on male nuptial gifts for food, and males provide nuptial gifts to females with larger ornaments. However, females with more moderately sized ornaments are more likely to mate, with larger ornaments coming at a cost to these females that experience higher rates of predation and reduced fecundity (Funk and Tallamy 2000; Gwynne et al. 2007; Wheeler et al. 2012; Gwynne et al. 2015). This means that there is potential for a trade-off between survival and mating success.

Factors influencing individual fitness show variation both in the short term, and over an animal's lifespan. For example, senescence (Bonduriansky and Brassil 2005), or the use of alternative reproductive tactics (Buzatto and Machado 2014; Painting and Holwell 2014b) can alter the extent to which sexual selection acts on individuals (Kokko et al. 2012), and this can be especially strong when access to mates is limited (Partridge and Farquhar 1983; Alcock 1996; Bonduriansky and Brassil 2002; Bonduriansky and Brassil 2005; Bonduriansky et al. 2008). Often in selection research only short-term trade-offs between natural and sexual selection pressures are possible to study. This necessarily overlooks how mating success may vary over an animal's lifespan, which may vary significantly between individuals in a population (McGraw and Caswell 1996; Bérubé et al. 1999; Marden et al. 2003; Robinson et al. 2006; Hayward et al. 2009). Sometimes (but not always, e.g. see Robson and Gwynne 2010), these measures of short-term mating success can limit or produce misleading information about an individual's fitness, and how sexual selection influences individuals (Partridge and Farquhar 1983; Banks and Thompson 1985; Scharf et al. 2013). For example, wild male antler flies *(Protopiophila litigata*) gained higher mating success early in their lives, but were not able to sustain this rate because of the cost of somatic damage, meaning that large size becomes a disadvantage at older ages (Bonduriansky and Brassil 2005). Understanding potential trade-offs between natural and sexual selection pressures provides a more complete understanding of how variation in traits and reproductive success is maintained in a population.

Female mating frequency can also vary, and the types of females males choose to mate with can impact male fitness (Bondurianky 2001; Herdman et al. 2004). But, this is frequently ignored in sexual selection studies (Clutton-Brock 2007, 2009). Males often choose to mate with specific females that display desirable traits as a way to increase their reproductive success (Bonduriansky 2001; Byrne and Rice 2006; Edward and Chapman 2011). The optimum choice made by males is for larger females with correspondingly high fecundity (Bonduriansky 2001; Bonduriansky and Brassil 2005). For example in the fiddler crab (*Uca mjoebergi*) males can distinguish between females of varying sizes and show a preference for courting larger females that produce larger clutches (Reading and Backwell 2007). Alternatively, males may increase their reproductive success by choosing females based on their reproductive status (i.e., virgin females (Simmons et al. 1994), or age (Xu and Wang 2009)). As a result of choosiness, mating patterns are often nonrandom (Jiang et al. 2013). Therefore, collecting corresponding measures of mating frequency for both males and females is important for gaining a more comprehensive understanding of selection in a population (Jones et al. 2006).

Studies of sexual selection in the wild that account for long-term variation and the lifetime reproductive success of individuals are important in conjunction with laboratory-based studies. With a long-term timeframe, the influence of sexual selection on numerous vertebrates has been studied in wild populations (for example: red deer (*Cervus elaphus*) (Clutton-Brock et al. 1997), Soay sheep (*Ovis aries*) (Robinson et al. 2006), bighorn sheep (*Ovis canadensis*) (Coltman et al. 2002), and many bird species (Székely et al. 2000; Emlen and Wrege 2004)). In comparison, insects and other invertebrates are rarely studied in the wild beyond short-term and point observations as they are often a challenge to observe and track in their natural habitats (Rodríguez-Muñoz et al. 2010). Therefore, model insect species such as *Drosophila*, field crickets (*Teleogryllus* spp.) and dung beetles (*Onthophagus* spp.) used for selection studies are typically observed within lab-based populations. Despite mating behavior in wild insects often being difficult to observe, there are some exceptions, including tree wētā (Kelly 2005), dance flies (Wheeler et al. 2012), and dung flies (Jann et al. 2000), where the challenges of collecting information on wild animals has been overcome. Although challenging, measuring lifetime reproductive success in the wild is the most accurate way to measure the fitness of an individual (McGraw and Caswell 1996). However, finding appropriate model species that can be directly observed in nature remains a challenge for behavioral ecologists conducting selection studies (Rodríguez-Muñoz et al. 2010; Zuk 2014).

New Zealand giraffe weevils (*Lasiorhynchus barbicornis*, Coleoptera: Brentidae) present an exciting opportunity for investigating sexual selection in the wild. They are found in

Figure 1. Wild giraffe weevils. (A) Three males fight for access to females within an aggregation by using their elongated rostrums as weapons. (B) A female giraffe weevil with her shorter rostrum used for drilling holes in wood to create oviposition sites. Photos by C J Painting.

aggregations on trees during the day, where they mate and females lay their eggs (Meads 1976; Painting and Holwell 2014c), making them easy to observe. Giraffe weevils are sexually dimorphic (Fig. 1), where males bear an elongated rostrum used in aggressive fights for mating opportunities (Painting and Holwell 2013, 2014a) (Fig. 1A), while females use their rostrum as a modified drill piece to prepare holes for egg-laying (Fig. 1B). The rostrum in males is known to display a steep positive allometry with body length, whereas in females the allometry is negative (Painting and Holwell 2013). Males also use alternative mating tactics, and can choose whether to employ sneaking or mate guarding and fighting tactics depending on the relative size of rivals (Painting and Holwell 2014b). The sex ratio in giraffe weevil populations is typically male-biased with intense mate competition (Painting et al. 2014), and as a result males use these alternative tactics to access females and gain mating opportunities (Painting and Holwell 2014b). Both sexes are highly polygamous and females do not show any evidence of precopulatory mate selection (Painting and Holwell 2013, 2014b). Additionally, both males and females are extremely variable in size: males can vary between 15–90 mm, and females between 13–50 mm in total body length (Kuschel 2003; Painting et al. 2014).

Extreme size variation could be expected to drive selection for large rostrum and body size (Painting and Holwell 2014b). A previous study by Painting and Holwell (2014b) investigated whether there was any evidence for selection on large size in male giraffe weevils. They used short-term observations of wild male giraffe weevils to count the number of times a focal male copulated with different females over an hour-long period (Painting and Holwell 2014b). Male contests are won 90% of the time by the larger contestant, strongly suggesting a large-male mating advantage (Painting and Holwell 2014b). Surprisingly, they found no evidence of sexual selection, based on mating success, driving rostrum length/body size, despite the extreme variation found in this species and the use of the rostrum as a weapon during fights.

The overall aim of this study was to build upon previous research to gain a deeper understanding of selection in giraffe weevils with reference to the interplay between size, sex, mating success, and survival. More specifically, our aims were to determine (1) how body size might predict survival and mating success in male and female giraffe weevils, (2) whether a size-related survival cost exists, where larger individuals may secure more matings but suffer a trade-off for lower survival rates, (3) whether body size is under stabilizing or directional selection, and (4) to investigate whether males have a preference to mate with larger females. We applied a range of collection and analysis techniques to explore our aims, including capture-mark-recapture techniques to look at size and sex related survival and recapture probabilities, and a traditional selection gradient approach using field-collected mating frequency data for both sexes over their approximate lifetimes. We expected that body size would be a strong predictor of mating frequency in both sexes, with males experiencing greater success due to their increased competitiveness in fights (Painting and Holwell 2014a), and females due to selection by males for potentially increased fecundity (Harari et al. 1999; Hunt and Simmons 2000; Bonduriansky 2001; Edward and Chapman 2011). As a result of this, we expected to find support for directional selection on size. However, we also predicted that larger males and females would experience a trade-off with survival due to potentially higher rates of predation (McLachlan et al. 2003; Gwynne et al. 2007; Gwynne et al. 2015), parasite loading (Zhang 1991; Kotiaho and Simmons 2001), or senescence (Bonduriansky and Brassil 2005). Finally, we predicted that larger and more competitive males would monopolize larger females leading to positive size-assortative mating.

Methods

Observations took place during summer in an area of native coastal broadleaf forest at Matuku Reserve (36° 51.92′S, 174° 28.32′E), west of Auckland City, New Zealand, known for its reliable and large giraffe weevil population (Painting and Holwell 2014c). Aggregations of giraffe weevils were located on sick or dead standing karaka trees (*Corynocarpus laevigatus*), the most common host species at Matuku Reserve (Painting and Holwell 2014c). For this study, when referring to the population we are referring to all of the weevils across the reserve. Whereas an aggregation refers to a subset of the population found locally on a tree. In this way, there is a single population that consists of many aggregations across the field site.

MARKING AND MEASURING

On each observation day (see below), all giraffe weevils on an observation tree were captured and a series of body size measurements taken using Rok digital callipers to the nearest 0.01 mm. All size measurements are very highly intercorrelated, including rostrum length (weapon size in males) (Painting and Holwell 2013). Due to this high correlation, we chose to use a single measure of body length (terminal end of elytra to the tip of mandibles) for both sexes as it is likely to provide the best estimation of fecundity for females, and presents us with almost identical information as using rostrum length (weapon size) for males. Following measurement, we marked individuals with a unique combination of five colored Queen Bee marking paints (Lega, Italy) on the pronotum and elytra (as in Painting and Holwell 2014c) so they could be identified in the future, and returned them to the same capture site. The role that these colors may have in making individuals more susceptible to predation is unknown. However, we believe that there should be no size or sex-related bias on predation due to the effect of the markings, as these were done chronologically (in the order that the individuals were first seen), which ensures that they were randomized for size and sex.

CAPTURE-MARK-RECAPTURE TECHNIQUE

To assess the survival and recapture probabilities of giraffe weevils, we used four different sets of capture-mark-recapture data, collected using two different recapture frequencies. This allowed us to comprehensively evaluate not only how sex and body size interact and influence survival and capture probability, but also to establish the best sampling strategy for this species.

The first two capture-mark-recapture datasets (“long-term”) were collected using similar sampling techniques over two consecutive adult breeding seasons. Our two long-term datasets included weekly capture events. The first occurred over a 20 week-period between October 24, 2011 and March 5, 2012 ($n = 841$ males, 562 females), sampling a total of 15 trees (i.e., different aggregations of weevils). Overall, 1403 unique individuals were identified over 3372 capture events that include individuals that were captured only once and those that were caught on multiple occasions. During this period the recapture probability for males was 43% and for females was 35%, and the average timeframe males were seen for (observed lifespan) was 13.6 (± 0.53 SE) days, and for females this was 15.7 (± 0.80 SE) days. Our second long-term dataset occurred over a 22 week-period in the following year between October 31, 2012 and April 2, 2013 ($n = 751$ males, 594 females), sampling a total of 13 trees. Overall, 1345 unique individuals were identified over 2145 capture events. During this period the recapture probability for males was 39% and for females was 38%, and the average timeframe males were seen for (observed lifespan) was 18.4 (± 0.84 SE) days, and for females this was 18.5 (± 0.80 SE) days. This dataset allowed us to investigate survival and recapture probabilities over the entire adult reproductive season.

In the following 2013/2014 season, we collected two additional (“short-term”) datasets using a more frequent (daily) sampling interval over a one month time frame. The first short-term dataset was collected when population abundance in Matuku Reserve was low across the entire reserve, based on Painting et al. (2014), and involved daily sampling from November 22 to December 22, 2013 (31 days, $n = 132$ males, 120 females), and overall we identified a total of 252 individuals over 981 capture events. The second dataset—with higher population abundance across the reserve (Painting et al. 2014)—involved daily sampling from the January 22 to February 23, 2014 (33 days, $n = 366$ males, 301 females), and overall we identified a total of 667 individuals over 2771 capture events. During these two sampling periods three different trees were visited and these trees differed between the two sampling periods.

SIZE-RELATED MATING SUCCESS

To investigate variation in giraffe weevil mating success over time we collected data on mating frequency while carrying out the mark-recapture sampling over the short-term periods in 2013–2014. Because we had two discrete observation periods we were able to compare long-term mating success in giraffe weevils at both high and low population abundances.

To track the mating history of individual giraffe weevils we conducted daily observations for one hour at each of the three mark-recapture trees. These hour-long observations were randomized and carried out during the highest daytime activity period for giraffe weevils between 0800 h and 1800 h (Painting and Holwell 2014c). On the first day, we marked and measured all visible individuals and then waited a minimum of two hours before carrying out observations to allow individuals to return to normal activity. On subsequent days, we conducted observations first, and then captured, marked, and measured any new individuals at the end. Care was taken to minimize any disturbance of individuals by maintaining a > 1 m distance from the aggregation and using close range binoculars (Pentax Papilio).

During the observation period all copulations were recorded along with the identity of the individuals to gain a measure of the number of unique copulations for each weevil present. At the conclusion of the hour, the aggregation site was thoroughly searched to ensure all individuals that may have been hiding in cracks or holes in the tree or under vegetation were recorded, and these we gave a count of zero copulations. Overall, we were able to calculate an average measure of daily mating success for each individual giraffe weevil present in the aggregations that were visited, which was calculated as the total number of matings observed (including zeros for days they were observed not to mate) divided by the number of days they were seen on. We chose not to use a measure of total copulation success because not all marked giraffe weevils at a site were observed every day, and we were unable to predict what their activity would be when they were not seen (i.e., they could have flown to another tree to find mates). Observations were not made on days of high rainfall when giraffe weevils become inactive and difficult to find (Painting and Holwell 2014c), which resulted in two days being missed during the first observation period, and three during the second, none of which were consecutive.

CAPTURE-MARK-RECAPTURE ANALYSES

The total number of individuals marked for each study period varied greatly as a result of the time frame (number of aggregations surveyed), and the substantial variation in giraffe weevil abundance at Matuku Reserve between years, and within a breeding season (Painting et al. 2014). Because individuals are rarely observed newly emerged as adults, or found dead, we were not able to confirm their first and last sightings as representing a complete lifespan for an individual. Additionally giraffe weevils can fly and are known to move between aggregation sites (Meads 1976), so it is not possible to establish true lifespan from observing them at a single aggregation site.

Given the open nature of giraffe weevil aggregations, we selected the Cormack-Jolly-Seber framework (Cormack 1964; Jolly 1965; Seber 1965) to estimate survival and recapture probabilities over time, while exploring potential effects of body size and sex (covariables). This approach estimates survival (φ) and recapture (P) probabilities, and allowed us to assess the effect of sex and body size on these parameters from individual encounter histories via maximum likelihood estimation methods (Lebreton et al. 1992; Williams et al. 2002). In this context, survival refers to “apparent survival” because in open population models, deaths are confounded with emigrations and births with immigrations (Williams et al. 2002). Recapture probability (p_i) is defined as the probability that a marked individual at sampling period i is captured or observed in the study area, and survival probability (φ_i) is defined as the probability that a marked animal at sampling period i, survives until period $i+1$ and remains in the population (does not permanently emigrate) (Williams et al. 2002). Based on these parameters, we built several models including constant (.), variations in time (t), and combinations for the parameters sex and body length (BL), to analyze the effect of body length on apparent survival and recapture probabilities according to sex. We used MARK 4.3 software (White and Burnham 1999), with a logit link function applied to all models. We calculated time-intervals daily to facilitate comparisons between the different datasets.

We evaluated the goodness of fit of the Cormack-Jolly-Seber model in U-CARE version 2.2 (Choquet et al. 2005) for each dataset using their respective global model (time-varying recapture and survival probability: φ_t p_t) (Supplementary Methods Tables S1 and S4) without including the covariables (body length and sex) because suitable tests for models that include individual covariates have not been developed yet (Cooch and White 2011). These assumptions include; (1) that every animal has the same probability of recapture, (2) that every marked animal has an equal probability of survival between recapture events, (3) that identification marks are neither lost nor overlooked, and are recorded correctly, and finally (4) the period of capture is instantaneous relative to the sampling interval (see Supplementary Methods for more details). We are confident that assumptions (3) and (4) were not violated during our surveys. However, for the short-term datasets, the goodness of fit tests (which evaluate assumptions (1) and (2) above) run presented significant violations to the model assumptions due to substantial heterogeneity in the data (Supplementary Methods Table S1). In an attempt to reduce this heterogeneity, we collapsed the data first into 3-day, and then 7-day intervals (Cooch and White 2011). However, the goodness of fit tests for both datasets still presented significant results, meaning that the assumptions of the models were not met (Supplementary Methods Table S2). The long-term resampling datasets collected by Painting et al (2014) (with weekly rather than daily sampling intervals) did not violate the Cormack-Jolly-Seber assumptions (Supplementary Methods Table S4), and therefore these datasets were better explained by the models. To avoid biases due to poor model fit, we chose to discard the short-term datasets and only used the long-term datasets collected by Painting et al (2014) in our subsequent capture mark recapture analyses.

The variance inflation factors ($\hat{c}$) for each dataset were estimated using median $\hat{c}$ in MARK (White and Burnham 1999; Cooch and White 2011). A $\hat{c}$ of 1 indicates a perfect fit of the model, with values greater than this interpreted as overdispersion, and smaller as underdispersion. The dataset from 2011–2012 presented a $\hat{c} = 1.24$ indicating minor overdispersion, whereas the 2012–2013 dataset presented a $\hat{c} = 0.784$ suggesting slight underdispersion. In both cases we adjusted the model selection procedure by using the $\hat{c}$ value to calculate a quasi-Akaike Information Criterion (QAICc) value, and used these values during model selection (Burnham and Anderson 2002). For both of these datasets, we then ran all of the possible models for recapture and survival. We ranked competing models using QAICc to select the model that best explained each dataset. Finally, we used the coefficients obtained from the most supported models to estimate apparent survival and recapture probabilities in relation to sex and body length.

Given that we were unable to use the capture-mark-recapture data from the two short-term observation periods due to issues with heterogeneity, we used a linear-mixed model (LMM) to investigate the relationship between observed lifespan (the number of days from the first to last sighting of an individual) and body size, sex, and observation period. In this way, we were able to determine whether the patterns identified in the long-term capture-mark-recapture studies in prior years were similarly found in the shorter term month-long study.

MATING SUCCESS ANALYSES

All selection analyses were done using R Version 3.5.0 (R Development Core Team 2018). We defined mating success in our models as the total number of times an individual was observed mating offset by the number of times (days) the individual was seen over the observation period, resulting in an average daily mating success for each individual. Individuals only observed once, or first recorded during the final week of observations were excluded from the analyses. If an individual was not observed on a given day this was treated as a missing data point and was not included in the calculation of average mating success. To determine if there is directional selection on body size in giraffe weevils, we used a negative binomial GLMM in the R package *lme4* (Bates et al. 2015) to investigate mating success for both male ($n = 309$) and female ($n = 235$) giraffe weevils, including observation tree as a random effect to account for potential variation between sites. The negative binomial model was necessary to account for the excess of zeros in our dataset where weevils were not observed mating during observations. Sex, body length, and observation period (low and high population density) were included in our full models, including possible interactions between sex and body length, and body length and observation period. All models were run using standardized size that was calculated by z-scoring the data. We simplified models using likelihood ratio tests to identify the most parsimonious model. In order to obtain directional and stabilizing selection gradients, we reran the models using separate negative binomial generalized linear models for each sex, including a quadratic term for body length, using the R package *MASS* (Venables and Ripley 2002). We used the equations described in Morrissey and Goudie (2016), which allowed us to calculate selection gradients and corresponding standard errors from nonlinear models. The estimates for these models were doubled to provide the final selection gradient values (Stinchcombe et al. 2008). We calculated the selection differential for each sex by investigating the covariance between relative mating success and size. Finally, we investigated the presence of size assortative mating in giraffe weevils. Our data included the first unique mating pairs observed during each observation period, so each giraffe weevil was represented once only (number of unique pairs = 191). Firstly, we calculated a Pearson's correlation coefficient (r_P) to investigate the prevalence of assortative mating. However, this test does not distinguish between a linear and "true," or an "apparent" assortative mating relationship. In cases of "apparent" assortative mating, the observed pattern is due to variance in male body size increasing or decreasing in relation to female body size (Crespi 1989; Arnqvist et al. 1996). To distinguish between these, we used a Spearman's rank correlation (r_S) to provide an index of heteroscedasticity (Arnqvist et al. 1996; Kelly 2014). This is a correlation of female body lengths, with absolute male body length residuals (obtained from a regression of male and female body length). This test allows us to explore whether with a change in female size there is an associated change in the variance of male size (i.e., as female size increases, is there lesser or greater variation in the sizes of the males that are pairing with these females). Here, a value < 0 indicates that large males have a relative "advantage" where they mate with females of all sizes, whereas a value > 0 indicates that small males have a relative "'advantage" where they mate with females of all sizes (Kelly 2014).

Results

SURVIVAL AND RECAPTURE

For our long-term recapture datasets we found that apparent survival was best described by a model varying by both sex and body length (Table 1). Additionally, recapture probability was best described by a model varying by both sex and body length, and in the 2011–2012 dataset this best-fit model also included time of the season (Table 1).

Overall, for both datasets, we found a significant effect of body size and sex on survival and recapture probabilities (Table 1). In both datasets, survival was consistently higher for females, which presented higher daily estimates compared to males (Table 2). Conversely, in both datasets males presented significantly higher daily estimates of recapture (Table 2).

The daily survival probability in both datasets increased consistently with size for both sexes (Fig. 2). However, this increase was slightly larger for males in the 2012–2013 dataset and survival probability was slightly higher in general for all sizes (Fig. 2). Whereas, we found the variation in female survival with size remained almost constant between the two seasons (Fig. 2).

Finally, we found that the daily recapture probability for both male and female giraffe weevils increased almost linearly with body size in both datasets (Fig. 2). However, recapture probability was on average lower in the 2011–2012 dataset for all male and female sizes (Fig. 2). In addition, we found that male giraffe weevils were consistently more likely to be recaptured than females of the same body size, but this difference was less in the 2012–2013 dataset (Fig. 2).

Table 1. Capture-mark-recapture model selection for survival and recapture of giraffe weevils during weekly sampling in 2011–2012 and 2012–2013.

	Survival	Recapture	QAICc	Δ QAICc	QAICc weight	Model likelihood	Parameters	Deviance
2011–2012 dataset	**φ (sex + BL)**	**P (t + sex + BL)**	**2130.92**	**0**	**0.90**	**1**	**24**	**2082.07**
	φ (t+ sex)	P (t + sex + BL)	2135.47	4.55	0.09	0.10	41	2051.01
	φ (BL)	P (t + sex + BL)	2140.63	9.71	0.01	0.01	22	2095.92
	φ (t+ sex)	P (t + sex)	2143.32	12.40	0	0	40	2060.97
	φ (sex)	P (t + sex)	2148.19	17.27	0	0	22	2103.47
	φ (t)	P (t + sex)	2149.41	18.48	0	0	39	2069.18
2012–2013 dataset	**φ (sex + BL)**	**P (sex + BL)**	**5262.45**	**0**	**1**	**1**	**6**	**5250.41**
	φ (BL)	P (BL)	5276.51	14.06	0	0	4	5268.49
	φ (BL)	P (sex + BL)	5278.21	15.76	0	0	5	5268.18
	φ (t+ sex)	P (t + sex)	5331.09	68.64	0	0	40	5249.48
	φ (t)	P (t + sex)	5333.61	71.16	0	0	39	5254.08
	φ (sex)	P (sex)	5334.97	72.52	0	0	4	5326.95

Models include the effects of body length (BL), sex, and time (t), asterisks indicate an interaction between terms. The top 6 models are listed for each dataset in order of QAICc rank, with the most supported model in bold first.

Table 2. Daily survival and recapture probability estimates for both male and female giraffe weevils based on the most supported models from data collected during both the 2011–2012 and 2012–2013 breeding seasons.

Year	Parameter	Estimate	95% Confidence interval
2011–2012	Male survival ($\emptyset_m$)	0.916	0.903, 0.928
	Female survival ($\emptyset_f$)	0.949	0.937, 0.959
	Male recapture (p_m)	0.382	0.318, 0.450
	Female recapture (p_f)	0.239	0.188, 0.298
2012–2013	Male survival ($\emptyset_m$)	0.929	0.922, 0.936
	Female survival ($\emptyset_f$)	0.951	0.945, 0.956
	Male recapture (p_m)	0.437	0.390, 0.484
	Female recapture (p_f)	0.374	0.330, 0.419

OBSERVED LIFESPAN

Similar to the capture-mark-recapture study, we found a significant positive relationship between body size and the observed lifespan of giraffe weevils monitored during the mating success observations ($\chi^2 = 19.26$, $P < 0.0001$; Table 3), but there was no significant difference in the observed lifespan of males and females ($\chi^2 = 0.516$, $P = 0.473$), or between the two observation periods ($\chi^2 = 3.343$, $P = 0.068$; Fig. 3).

MATING SUCCESS

Rates of polygyny and polyandry were high over both observation periods: 65% (202 of 309) males were observed to mate multiple times over one hour, and for the females the number was greater with 77% (181 of 235) observed to mate more than once. We considered variation in average daily mating success using three variables: body length, sex, and observation period. We found no significant difference in mating success between the two observation periods, so this term was dropped from the model ($\chi^2 = 1.631$, $P = 0.202$). The best-supported model included a significant interaction between body length and sex, as shown by the likelihood ratio test comparing an interaction model to a full additive model ($\chi^2 = 27.766$, $P > 0.001$, $\Delta\text{AIC} = 25.77$; Table 4).

Rerunningthese models using separate GLMs with Negative Binomial error for each sex provided selection gradients that show a significant positive relationship between mating success and size for males and females, giving evidence of increased female mating frequency with size that is likely to represent selection by males for larger females (Table 5). Females with a body length of 20 mm mate on average with 0.8 males/hour/day, compared

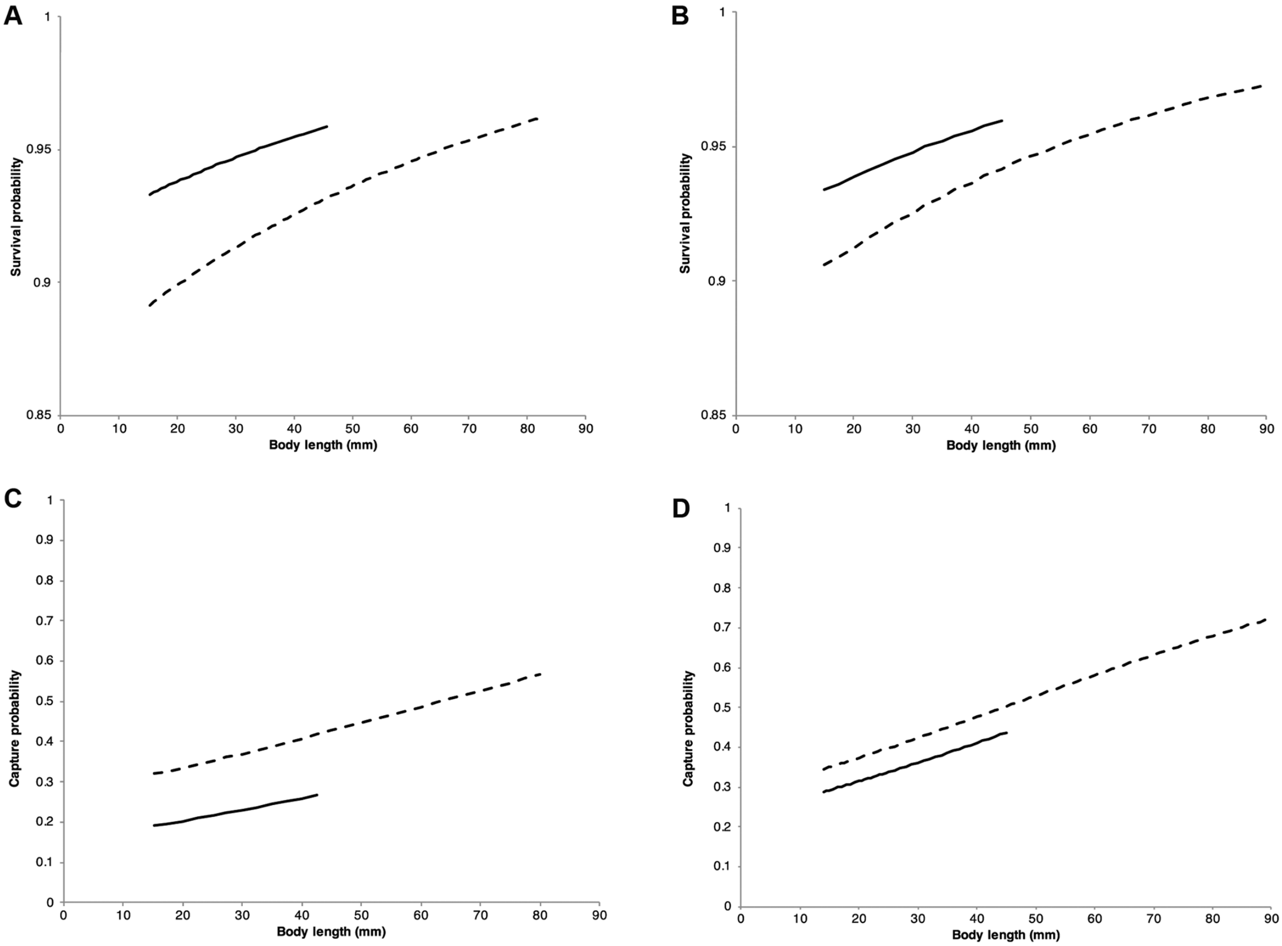

Figure 2. Survival and capture probabilities of male (dashed line) and female (solid line) giraffe weevils by body length derived from the most supported models for data collected in (A and C) 2011–2012 and (B and D) 2012–2013.

Table 3. Linear-mixed model estimates of size (body length) from the best-supported model for observed lifespan in giraffe weevils.

Variable	Estimate	SE	*t*	*P*
Intercept	8.769	1.211	7.239	<0.0001
Size	0.133	0.030	4.408	<0.0001

to those with a body length of 40 mm that mate on average with 1.65 males/h/day. Similarly males with a body length of 20 mm on average mate with 0.5 females/h/day, compared to those with a body length of 80 mm that mate on average with 0.75 females/hour/day. In addition, we found that on average, female giraffe weevils mate almost twice as frequently as males (Table 4, Fig. 4). However, we did not find any evidence for stabilizing selection on size for either male of female giraffe weevils (Table 5).

SIZE ASSORTATIVE MATING

A Pearson's correlation showed that within observed mating pairs of giraffe weevils, there was a significant positive relationship between male and female body lengths ($r_P = 0.27$, $N = 189$, $P < 0.001$) (Fig. 5). A Spearman's rank correlation also showed a positive index of heteroscedasticity ($r_S = 0.95$, $P < 0.001$) between male and female body lengths. This suggests that smaller males pair with females of all sizes, and larger males only with larger females.

Discussion

We found evidence for directional selection on body size for male giraffe weevils with larger individuals having higher average mating success (Table 4, Fig. 4). In addition, we found that males choose to mate with larger females (Fig. 5). Contrary to our prediction, we found no apparent survival cost to being large as bigger bodied individuals of both sexes have a higher daily survival rate (Fig. 2). Larger giraffe weevils mate more frequently and survive for longer in a population, suggesting an accumulation of mating success benefits to bigger individuals. Beyond a higher mating success, large males may increase these benefits further via size-assortative mating. Given that there is often a strong

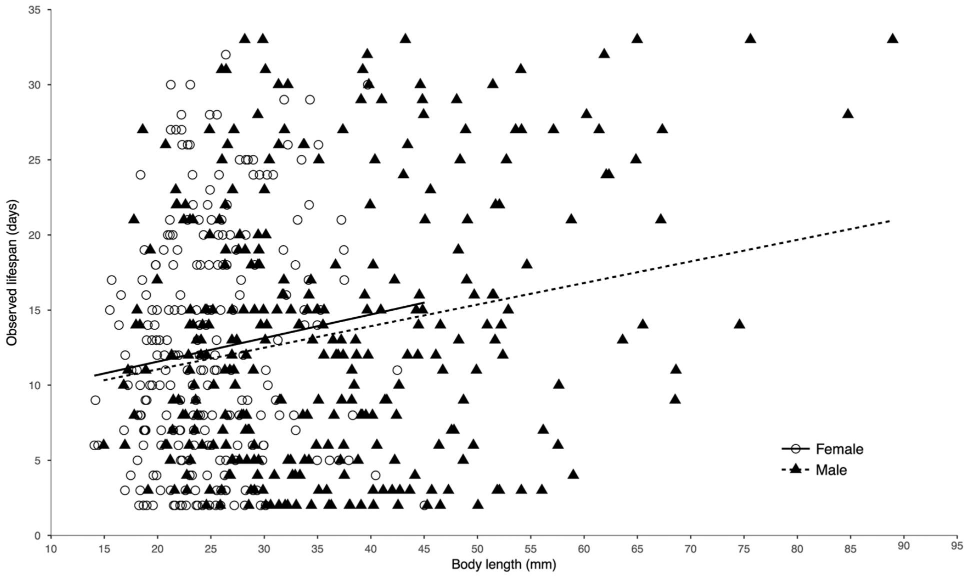

Figure 3. Relationship between observed lifespan (days) with body length for male and female giraffe weevils.

Table 4. Generalized linear-mixed model with negative binomial error estimates of body length and sex from the best-supported model for average mating success in giraffe weevils.

Variable	Estimate	SE	*z*	*P*
Intercept	0.25	0.10	2.61	0.009
Standardized body length	0.45	0.08	5.52	<0.0001
Sex	–0.85	0.07	–12.13	<0.0001
Standardized body length × sex	–0.35	0.09	–4.02	<0.0001

correlation between female body size and fecundity in other animal species (Honěk 1993; Calvo and Molina 2005; Saeki et al. 2005; Simmons and Emlen 2008), mating with large females may increase overall male fitness. For example larger female beetles often have larger and more abundant eggs (Saeki et al. 2005; Kajita and Evans 2010). Furthermore, male Japanese beetles (*Popillia japonica*) when given the choice will preferentially mate with larger and more fecund females (Saeki et al. 2005). Our size assortative mating analyses revealed that male giraffe weevils of all sizes appear to prefer mating with large females, but large males that are more competitive within a population are more likely to secure those large females and therefore increase their fitness further (Fig. 5).

This study is a rare example of using long-term tracking data for individual insects in the wild to address questions about sexual selection and survival. Previously, Painting and Holwell (2014b) measured mating success in male giraffe weevils using point observations similar to our daily observation technique. They expected to find evidence for selection on body size given the extreme variation in size and strong sexual dimorphism in giraffe weevils (Painting and Holwell 2014b). Surprisingly however, they found no evidence for selection, and as a result, Painting and Holwell (2014b) predicted that additional fitness trade-offs not measured in their study were at play. They concluded that sexual selection overall was a driving factor behind male size, but other factors such as lifespan, sperm competition, and population density may interact to influence male reproductive success and that more extensive observations were necessary. Our study that tracks individual giraffe weevils—allowing us to calculate their average mating success over the duration of a large proportion of their lifetime—provides evidence for directional sexual selection for size in giraffe weevils. Larger males have an increased competitive advantage as they are able to more successfully guard females and win the majority of fights against smaller competitors, gaining access to more mating opportunities and increasing their fitness (Painting and Holwell 2014a). It is also possible that the strength of selection varies from year to year for a population, which might explain somewhat the difference in findings between the two giraffe weevil studies with different observation lengths (Kasumovic et al. 2008; Siepielski et al. 2009; Cornwallis and Uller 2010). However, our investigations appear to have demonstrated overall that investigating mating success over an extended time frame can reveal selection on traits not seen in shorter term studies.

Contrary to our initial prediction, one of the most surprising findings from this study is that both sexes of giraffe weevil have increasing survival probabilities with larger body size. This is surprising as one expectation might be that bigger animals are subject to a trade-off where they may be more successful at securing copulations but experience lower survival due to increased

Table 5. Estimates of linear (β) and quadratic (γ) selection gradients from a negative binomial GLM regression of relative mating success on standardized female and male body size.

	β (± SE)	*P*	γ (± SE)	*P*	Selection differentials
Females	0.26 (0.04)	<0.0001	–0.003 (0.05)	0.95	1.40
Males	0.18 (0.04)	<0.0001	–0.01 (0.04)	0.76	2.12

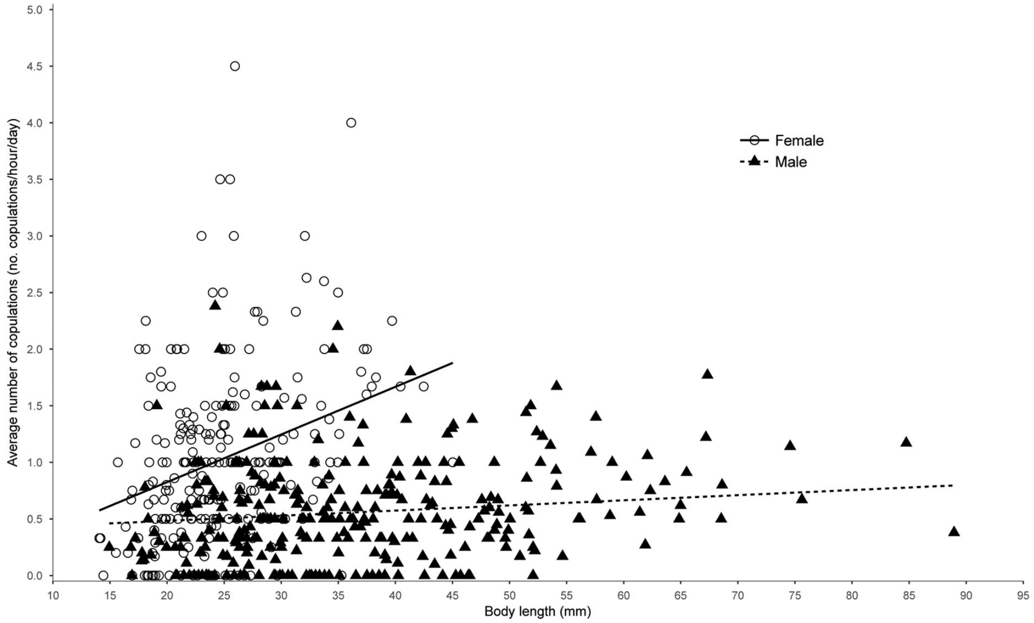

Figure 4. Relationship between mating success (average number of matings per hour per day) with body length for male and female giraffe weevils.

mortality as a result of encountering factors such as higher predation (Alcock 1996; Hedenström and Rosén 2001; McLachlan et al. 2003; Ercit and Gwynne 2015; Tammaru et al. 2018) or parasite loads (Zhang 1991; Kotiaho and Simmons 2001). Individuals who live longer are likely to experience more mating opportunities, and therefore benefit from a higher lifetime fitness. If smaller males have a higher survival probability on average, but a lower competitive advantage, survival is thought to potentially explain some of the size variation found among males of a species as smaller males can, over their lifetime, achieve a mating success comparative to larger and more competitive males (Zahavi 1975; Forsman and Appelqvist 1999; Romiti et al. 2015). Higher survival rates have been found for smaller individuals that invest less in costly fighting and mate guarding behaviors, such as in the European stag beetle (*Lucanus cervus*) and freshwater isopod (*Asellus aquaticus*) (Zahavi 1975; Benesh et al. 2007; Romiti et al. 2015). Alternatively, in species that do not engage in fighting behaviors, larger individuals may live for longer (Ohgushi 1996; McConnell and Judge 2018). For example, larvae of the mealworm beetle (*Tenebrio molitor*) fed higher quality diets develop into larger and longer lived adults–-however unlike the giraffe weevils, these larger males do not achieve increased copulation success (McConnell and Judge 2018).

In giraffe weevils, there appears to be no size-related trade-off between survival and mating success. One reason that larger giraffe weevils have higher survival may be that they have higher energy reserves because of the length of time (two or more years) they spend as larvae building up fat reserves (Van Dijk 1994; Painting and Holwell 2014c). Although our analyses cannot disentangle the difference between emigration and death, the fact that we see the same trend for both sexes suggests that survival rather than site fidelity is at play. This is because we would not anticipate a size-biased emigration for females because they are not mate-limited—as aggregation sex-ratios are consistently male biased (Painting et al. 2014)—and also because females select a site based on its suitability for oviposition. However, there is a possibility that if females are resource limited that they may undergo some size-biased dispersal, especially if small females are less competitive and must disperse to find other oviposition sites. It is possible however that small males show reduced site fidelity and higher emigration as a mating tactic if competition is high and they are not successful in gaining copulations in their

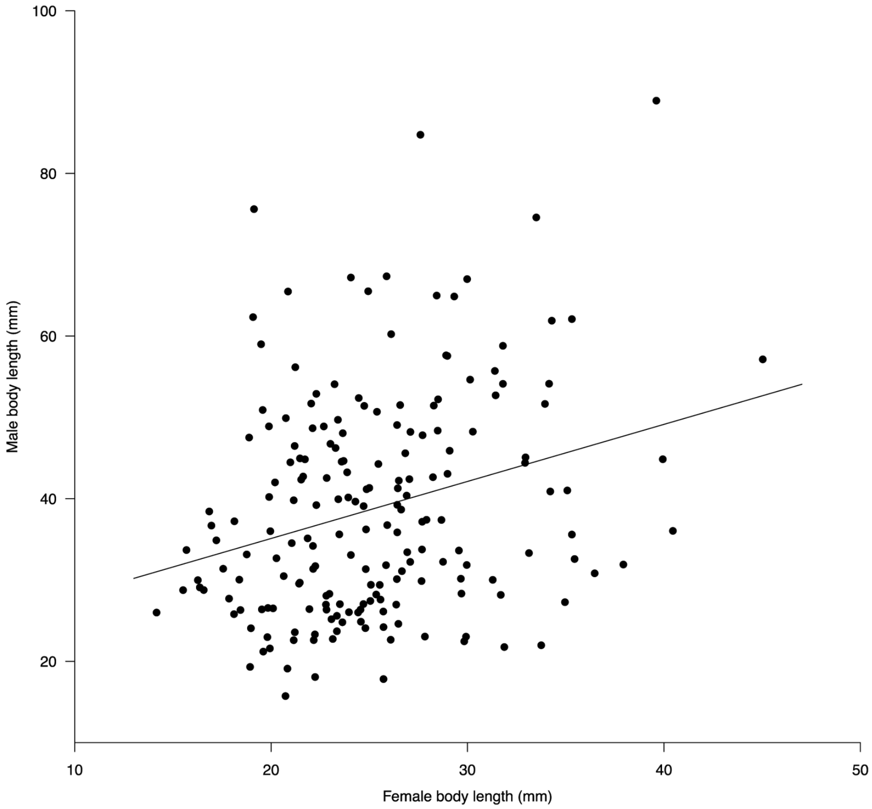

Figure 5. Correlation of male body length to female body length in observed unique mating pairs of giraffe weevils.

current aggregation. Smaller individuals may be better adapted to dispersing by flight as they are lighter and faster fliers than larger males (Kawano 1997; Romiti et al. 2015).

Despite finding evidence for positive selection on male body size, we see a large amount of variation in our mating success data and a relatively weak positive selection gradient. It is likely that studying a wild population is one cause of this variation, because in the field there are many other factors at play that can affect an individual's opportunity to mate. Other studies examining mating success in the wild have found similar evidence of weak selection for trait size with similar high variation (Reid et al. 2004; Amin et al. 2012; Hämäläinen et al. 2012). For example, although male song sparrows (*Melospiza melodia*) with greater song repertoires achieve on average a higher mating success, there is high variability in mating success among individuals (Reid et al. 2004). This is most likely a result of highly complex pair formation processes in this species (Reid et al. 2004). Theory predicts that a population's variation in mating success will increase as a result of alternative reproductive tactics increasing the potential for sexual selection (Møller and Birkhead 1994; Neff 2001). However, alternative tactics have also been shown to decrease the opportunity for sexual selection, especially when males are highly polygynous (Jones et al. 2001). This result was demonstrated in the sand goby (*Pomatoschistus minutus*), where sneaking behavior was found to decrease the opportunity for sexual selection because guarding males were unable to monopolize females (Jones et al. 2001). As small male giraffe weevils employ sneaking tactics to gain additional copulations, this may lower the opportunity for selection in this species. However, despite this variability, as we have demonstrated here, even a slightly higher mating success and greater fitness can drive selection, which appears to only require a marginal difference to work upon.

Beyond this reasoning, a recent investigation of the relative influence of luck on reproductive success by Snyder and Ellner (2018) found that chance or "luck" can play a large role in reproductive success, and may be more predictive than trait variation in some cases. This is an interesting concept with reference to our findings, where the positive relationship between male mating success and body size appears to be largely driven by the largest males (larger than approximately 50 mm, Fig. 2). This fundamentally makes sense, as the largest males in a population have a competitive advantage and will be able to monopolize females (and therefore rely less on luck) in these male-biased aggregations. The smaller males however, are more likely to rely on an element of luck to gain matings, where they might "chance upon" an unguarded female and mate with her. This would result in the large variation that we see in our data for males of smaller sizes, where males of the same size might vary greatly in their mating success due to luck playing a large role in this system (Snyder and Ellner 2018). In addition, giraffe weevil aggregations are dynamic, at any point in time there is a chance for a male of any size to be the largest male present on a tree. At this point, that male will have the highest potential for mating success as he will be the most competitive male present in the aggregation. Again, this concept is influenced greatly by the element of luck. Even if that male is of smaller than average size in terms of the entire local population, he might simply be lucky to arrive at an aggregation and become the largest male present.

Alongside directional selection on male giraffe weevil size, we have found a strong positive relationship between mating success and female body size. Although the potential benefits of polyandry in this species are unknown, this relationship is most likely to be driven by precopulatory male mate choice, as females almost never reject male mating attempts or appear to play a role in mate choice (Le Grice pers. obs.). Additionally, among mating pairs of giraffe weevils we found a strong positive correlation between male and female size. Further, we found that larger males more commonly mated with larger females, however smaller males mated with any sized female, indicating that they might often be competitively limited to mating with those smaller females. Size assortative mating is a common phenomenon in a range of taxa (Elwood et al. 1987; Arnqvist et al. 1996; Jiang et al. 2013). Generally, the best way males can increase reproductive success is to mate more frequently, however, another option is to choose to mate with larger, more fecund females (Harari et al. 1999; Hunt and Simmons 2000; Bonduriansky 2001; Edward and Chapman 2011). Although females are typically considered the choosy sex when it comes to mate choice, males can be equally choosy (Bonduriansky 2001; Wedell et al. 2002; Edward and Chapman 2011). This is often the case in situations when males can assess female fecundity by a physical attribute such as size (Wedell et al. 2002; Hoefler et al. 2009; Tudor and Morris 2009; Edward and Chapman 2011). In the dung beetle *Onthophagus taurus*, there is a direct linear increase in brood mass with female size (Hunt and Simmons 2000). Furthermore, in this species where there is also large variation in male size, mating with larger males also increased brood size, providing evidence for increased reproductive output being linked with both male and female size (Hunt and Simmons 2000). Because many of the elements defined above are found in giraffe weevils, including a male-biased sex ratio with fierce competition between males, and extreme variation in female size, it is possible that males will also attempt to increase their reproductive success by choosing larger females that may reward them with higher fecundity (Verrell 1985; Herdman et al. 2004; Nandy et al. 2012).

Although positive mating assortment is typically assumed to offer males increased reproductive success, high rates of size-related polyandry may deteriorate the benefits of mating with large females (Sih et al. 2009; McDonald et al. 2013; McDonald and Pizzari 2016). Often in polyandrous populations the intensity of sperm competition directly determines male reproductive success, so as sperm competition increases a male's share of paternity correspondingly decreases (Parker and Pizzari 2010; Collet et al. 2012; Kvarnemo and Simmons 2013; Parker and Birkhead 2013). Further, if the level of polyandry varies across the female population, males that mate with more polyandrous females are subject to higher sperm competition and potentially lower reproductive success (McDonald and Pizzari 2016). In giraffe weevils, we found that bigger males tend to mate more frequently with bigger females and that both bigger males and females mate more frequently on average. As a result, bigger males are likely to be facing a high intensity of sperm competition, which may lower their reproductive success and weaken the intensity of selection on weaponry and body size (McDonald and Pizzari 2016). Overall, giraffe weevils offer an exciting opportunity to explore the complex interplay between exaggerated weaponry, alternative mating tactics, and polyandry. In the future, studies that address reproductive success using genetic parentage techniques will allow us to further tease apart these factors.

AUTHOR CONTRIBUTIONS

Rebecca J. LeGrice: Study conception and design, data collection, analysis, manuscript writing.
Gabriela Tezanos-Pinto: Data analysis, manuscript writing.
Pierre de Villemereuil: Data analysis, manuscript writing.
Gregory I. Holwell: Study conception and design, manuscript writing.
Christina J. Painting: Study conception and design, data analysis, manuscript writing.

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DATA ARCHIVING

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Results from the goodness of fit tests run in U-CARE for 'short-term' capture-mark-recapture datasets collected with daily recaptures over two one-month surveys, November-December (Nov-Dec) and January-February (Jan-Feb), during one adult giraffe weevil breeding seasons (2013-14).
Table S2. Results from the goodness of fit tests run in U-CARE for capture-mark-recapture datasets collected with collapsed data from daily recaptures over two one-month surveys, November-December (Nov-Dec) and January-February (Jan-Feb), during one adult giraffe weevil breeding seasons (2013-14).
Table S3. Results from the goodness of fit tests run in U-CARE for the short-term capture-mark-recapture datasets collected with daily recaptures over a one-month surveys during January-February (2013-14) and run separately by sex.
Table S4. Results from the goodness of fit tests run in U-CARE for 'long-term' capture-mark-recapture datasets collected with weekly recaptures over 20 weeks during two different adult giraffe weevil breeding seasons (2011-12 and 2012-13).