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Cite this article: Nason SE, Kelly CD. 2020

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Proc. R. Soc. B **287**: 20200975.

<http://dx.doi.org/10.1098/rspb.2020.0975>

Received: 29 April 2020

Accepted: 7 July 2020

Subject Category:

Evolution

Subject Areas:

behaviour, evolution

Keywords:

sexual selection, polymorphism,
alternative mating strategies, phenotype

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Equal fitness among alternative mating strategies in a harem polygynous insect

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Alternative mating strategies are widespread among animal taxa, with strategies controlled by a genetic polymorphism (Mendelian strategy) being rarer in nature than condition-dependent developmental strategies. Mendelian strategies are predicted to have equal average fitnesses and the proportion of offspring produced by a strategy should equal the equilibrium proportion of individuals representing the strategy in a population. Developmental strategies are not expected to produce offspring in equilibrium proportions; however, whether the alternative phenotypes should have equal average fitness is debated. The Wellington tree wētā (*Hemideina crassidens*) (Orthoptera: Anostomatidae) is a harem polygynous insect in which intense sexual competition has favoured the evolution of three alternative mating strategies that differ in weapon size and the ability to fight for control of harems. Here, we use molecular genotyping to test the hypothesis that the alternative strategies in this species are maintained by having equal relative fitness and that morphs produce offspring in equilibrium proportions. As expected, the average relative fitness of the three strategies did not significantly differ and the proportion of offspring produced by each morph is equal to the frequency of that morph in the population. Our results support the hypothesis that the alternative male morphs in *H. crassidens* represent Mendelian strategies.

1. Introduction

Sexual selection is arguably nature's most powerful evolutionary process in that it can overcome natural selection to produce incredible phenotypic diversity within and between the sexes and across taxa in remarkably short periods [1–3]. A taxonomically widespread and common evolutionary outcome of intense sexual selection is the production of alternative phenotypes in which individuals within a sex adopt different strategies to successfully mate [2,4,5]. In fact, some of the most dramatic examples of alternative phenotypes in nature are related to differences among males in reproductive behaviour, morphology, physiology and life history [2,4–6]. In most species in which males express alternative strategies the conventional males are typically dominant and territorial and court females whereas the unconventional males are subordinate and non-territorial and adopt sneak mating tactics to achieve copulation. Although alternative mating strategies (AMSs) have fascinated biologists for almost two centuries, explaining their evolution, expression and maintenance in natural populations remain some of the most contentious issues in evolutionary biology [2,4,5,7–9].

AMSs can be expressed, for example, as a result of a genetic polymorphism or via a condition-dependent developmental pathway. Genetically polymorphic AMSs are hypothesized to be influenced by a few loci of major effect with males exhibiting within-population Mendelian segregation and are expected to arise when environmental cues predicting breeding opportunities are absent [2]. Mendelian strategies are expected to have equal fitness [2]. Moreover, the equilibrium proportion of males representing each strategy in a population should equal the proportion of offspring produced by that strategy [10] and morphs should persist within a population in approximately stable proportions [11].

Examples of Mendelian strategies include the lekking ruff *Philomachus pugnax* [12], *Paracerceis sculpta* marine isopods [13], the pygmy swordtail *Xiphophorus nigrensis* [14], the damselfly *Mnais costalis* [15], the acarid mite *Rhizoglyphus robini* [16] and the side-blotched lizard *Uta stansburiana* [17]. Shuster & Wade [2] argue that Mendelian strategies are likely to be more common in nature than is currently recognized.

By contrast, West-Eberhard [9] argues that Mendelian strategies are likely to be exceedingly rare because selection should instead favour flexible developmental strategies underpinned by polygenic, condition-sensitive regulatory mechanisms. That is, AMSs are more likely to be the result of reaction norms in which the adult male phenotype is a plastic response of his genome to the environment [18] or to maternal effects [19]. A developmental strategy is predicted to arise if environmental cues reliably predict the nature of the contests that will determine future mating opportunities [2].

Why developmental AMSs persist in natural populations once evolved is a controversial issue in evolutionary biology [2,8,9]. The focus of the controversy is whether average fitnesses need to be equal among the different strategies [2,4,20,21]. Confusion over whether equivalent fitnesses are necessary originates from the voluminous data collected in wild populations showing conventional (i.e. harem-holding) males to have greater mating success than unconventional (i.e. subordinate) males [2,3,5]. Dawkins [22] famously observed that in such cases unconventional males are simply 'making the best of a bad job' because even though they accrue less success than conventional males they are at least gaining more fitness than if they had never mated. Gross [4] formally modelled this verbal explanation as the status-dependent selection (SDS) hypothesis, a model suggesting that the persistence of polymorphisms in a population requires neither equal fitnesses nor genetic differences among morphotypes if individuals can attain the status (e.g. body condition, age, body size etc.) providing the greatest fitness.

Others, however, find this line of reasoning untenable and argue that average fitnesses must be equal and have a genetic basis because, if not, polymorphisms cannot be maintained in a population over time [2,21,23,24]. The foundation of this argument is that developmental AMSs are likely to be underpinned underpinned by threshold traits, meaning that the expression of a discrete phenotype depends on where an individual lies with respect to the threshold of a liability trait (e.g. level of hormone titre) [25]. If an individual lies below the threshold then one phenotype will be expressed while lying beyond will cause the expression of the alternative phenotype. Threshold traits are influenced by both the environment and, importantly, many genes [25]. Abundant evidence shows that threshold traits are heritable and so stabilizing selection will act on the threshold's underlying genetic variation to eliminate those variants that fail to respond appropriately to the prevailing environmental conditions, which would ultimately confer less fitness on that genotype [2]. Only variants that express the appropriate phenotype within a given environment should persist in the population [2]. Unlike Mendelian strategies, males expressing developmental strategies are not expected to produce offspring in equilibrium proportions. No study has yet empirically shown developmental strategies to have equal fitnesses.

The conclusion that developmental alternative strategies generally have unequal fitness payoffs [3,4] is, however, premature as morph-specific fitness estimates are typically biased

and inaccurate [3]. First, field studies of alternative mating strategies often fail to sample unsuccessful males from each strategy. By excluding unmated males from analyses of fitness, the average fitness will be overestimated and the variance in fitness will be underestimated for each morph [1]. Second, mating success, a popular proxy measure of fitness, does not necessarily translate into fertilization success due to post-copulatory processes within the female reproductive tract [26,27]. This will have particularly important implications on fitness calculations if subordinate males are superior sperm competitors. Third, studies conducted over short temporal scales will be misleading if alternative morphs are active at different times of the day or breeding season, or have different reproductive lifespans [28].

The Wellington tree wētā (*Hemideina crassidens*) is a harem polygynous, nocturnal and flightless orthopteran that is endemic to New Zealand [29]. In *H. crassidens*, tree cavities are used by both sexes as diurnal refuges from predators and because these cavities can be limiting in nature, several wētā can concurrently reside in a cavity (hereafter, 'gallery') [30–33]. Such refuging often leads to harem formation [30,31,34]. However, the time that harems and the resident male remain together is typically less than 3 days, on average, and is positively related to harem size [31]. Harem formation provides males with an opportunity to increase their reproductive success by monopolizing females [31,35,36]. Indeed, males use their enlarged mandibles in combat with other males for control of female-occupied galleries [31,35,37] and males with larger mandibles enjoy greater harem success [38,39]. Strong sexual selection has apparently favoured the evolution of two alternative strategies in this species [40,41]. Conventional males mature at the 10th instar (as do females) while unconventional males precociously mature at either the 8th or 9th instar [40]. The 10th instar males possess larger bodies and larger mandibular weaponry, 8th instar males possess smaller bodies and smaller weaponry, whereas 9th instar males are intermediate to the other two morphs [41]. The 10th instar males have significantly greater resource-holding potential than the other morphs and consequently tend to reside with larger groups of females, 8th instar males circumvent the defences of larger males and sneak copulations and 9th instar males appear to be a jack-of-all-trades that can sneak or fight depending on the situation [33,37–39]. The three male morphs persisted in stable proportions across 7 years in our study population [41], which suggests that morph frequency in this population is at or near equilibrium.

In this study, we use molecular parentage assignment to quantify the reproductive success of the three alternative mating strategies in male *H. crassidens*. Morph-specific fitnesses are then used to test the prediction that the alternative mating strategies in *H. crassidens* are genetic polymorphisms that are maintained at an evolutionarily stable equilibrium. We predict that the average relative fitnesses among the morphs do not significantly differ [2] and use long-term data on morph frequency to test the Gross & Charnov [10] model that the equilibrium proportion of males representing each strategy in the population equals the proportion of offspring produced by that strategy.

2. Methods

We collected adult tree wētā from 95 galleries on Te Pākeka/Maud Island (New Zealand), a scientific reserve free of introduced

predators, during March–April 2017. Following Kelly [38], we sampled galleries in deadwood on the forest floor (none were occupied), inspected artificial nest boxes ($n=7$ occupied) and destructively sampled living trees ($n=88$ occupied). For each wētā found in a gallery, we noted its lifestage (juvenile or adult), sex, and the number and sex of its gallery cohabitants. The length of the head and left and right hind femura were measured to the nearest 0.01 mm using digital calipers (Fisher Scientific, St Laurent, Canada). Harem success of each male was defined as the number of females residing with a male in a gallery [38]. Multiple males were found residing together in 10 galleries. In five of these cases, a smaller morph(s) was found with a larger morph and in these cases harem ownership was assigned to the largest morph because larger morphs have greater resource-holding potential and typically win fights for gallery ownership versus smaller morphs [37–39,42]. In the remaining five cases, two males of the same morph were found together (9th with 9th, $n=1$; 8th with 8th, $n=4$). In these cases, gallery ownership was assigned to the male with the largest mandibles because mandible length is indicative of resource-holding potential [37,42]; however, a harem was present in only two of these cases (9th and 9th resided with five females; 8th and 8th resided with one female).

The middle left leg of each wētā was removed and preserved in 80% ethanol for genotyping. Males were released into nature immediately after processing while females were placed in 5 l buckets for 1–2 weeks for oviposition. Each bucket was provisioned with oviposition substrate (moist vermiculite), a refuge and a piece of apple (replaced every 2–3 days). Females were tissue-sampled (removal of the left middle leg) after oviposition to avoid adverse effects of leg removal on egg laying behaviour. Eggs were collected from the vermiculite and transported to the laboratory at the Université du Québec à Montréal where they were kept on moist vermiculite in deli containers in a temperature- and humidity-controlled growth chamber until hatching. Newly hatched nymphs and unhatched eggs were preserved in 95% ethanol for genotyping.

Adults and offspring were genotyped at four polymorphic microsatellite loci by using primers developed for *Hemideina* species [43,44] including *H. crassidens* [45]. Paternity was assigned with 95% confidence using CERVUS 3.0 [46]. As the probability of failing to exclude an incorrect parent was not much changed when any one locus was removed, we included individuals in the paternity analysis if they were successfully typed at three or more loci (95.8% of all genotyped offspring).

We categorized males to one of three morphotypes based on the morph-specific head length ranges calculated by Kelly & Adams [41] (see also [38]). We examined morph-specific differences in harem success by using generalized linear models with male morph entered as a fixed effect and harem success entered as the response variable. We then similarly examined morph-specific differences in fitness by using generalized linear models with male morph entered as a fixed effect and relative reproductive success entered as the response variable. We standardized reproductive success (relative fitness) by dividing each individual's reproductive success by the mean for males in this population. Negative binomial error distribution was used for both models because the response variables were over dispersed. Alternative morphs might compensate for their poorer harem success by being more sperm competitive and thus fertilizing a greater proportion of eggs per brood than their 10th instar counterparts. We tested whether the morphs differed in the mean proportion of offspring sired per brood by using a linear mixed model (with female ID entered as a random effect) with morph entered as a fixed factor.

We tested Gross & Charnov's [10] model that the equilibrium proportion of males representing each strategy in the population equals the proportion of offspring produced by that strategy by first pooling the morph frequencies observed in this study with

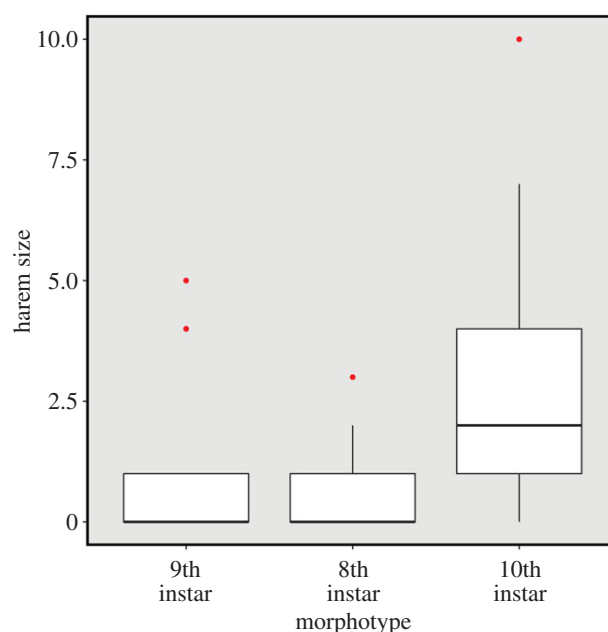


Figure 1. Boxplots of harem success of each male morphotype in *H. crassidens*. The box represents the lower (25%) and upper (75%) percentiles, the solid dark horizontal line is the median, the upper whisker extends from the hinge to the largest value no further than $1.5 \times$ interquartile range and the lower whisker extends from the hinge to the smallest value at most $1.5 \times$ interquartile of the hinge. Outliers are denoted as red dots. Sample sizes are $n=53$ (8th instar), $n=23$ (9th instar) and $n=9$ (10th instar). (Online version in colour.)

those from six other years (published in [41]) to obtain updated average morph frequencies in this population. We then examined whether the proportion of total offspring sired by each morph fell within the 95% confidence interval of their respective frequency in the population.

All statistical tests were conducted at $\alpha=0.05$ significance level, means are $\pm 95\%$ confidence limits and p -values from linear models are based on type III sums of squares. All statistical analyses were performed in R v. 3.6.1 [47].

3. Results

We collected a total of 85 males and 99 females from 95 galleries (see [45] for details of gallery occupation). The frequency of 8th (0.47), 9th (0.29) and 10th (0.24) instar males in our sample did not differ from previous frequency estimates for this population ($\chi^2=0.27$, d.f. = 2, $p=0.875$ [41]). Multiple males were found residing in the same cavity on 10 occasions [45]: a representative of each of the three morphs co-resided in a gallery in one case (with seven females present), 8th with 8th in four cases (no females were present in three cases and one in the other), 9th with 9th in one case (five females present), 8th with 9th in two cases (one female present in each case) and 8th with 10th in two cases (4 and 1 females present, respectively) [45].

As predicted, males differed significantly in harem success ($\chi^2=22.09$, d.f. = 2, $p<0.0001$) with 9th instar males having significantly larger harems than 8th instar males ($z=2.27$, $p=0.02$) but significantly smaller harems than 10th instar males ($z=-2.27$, $p=0.02$) (figure 1).

About 45 females laid a total of 416 eggs ($\bar{x} \pm se$, 9.24 ± 1.68 eggs per female) of which 267 hatched (from 21 females).

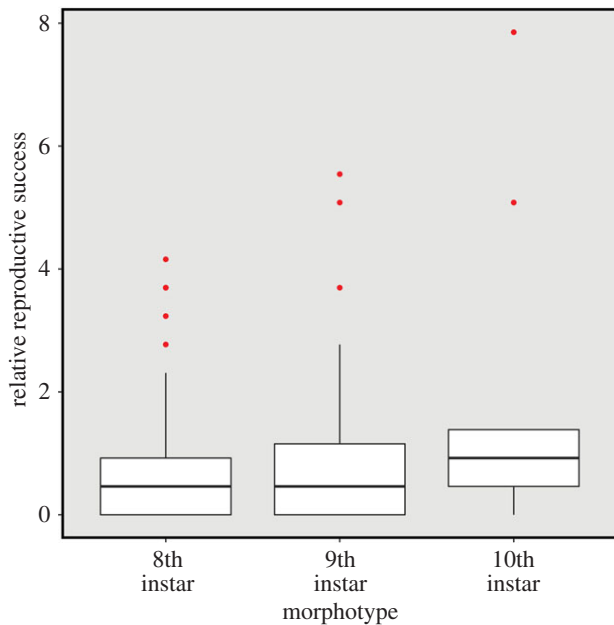


Figure 2. Boxplots of relative reproductive success (fitness) of each male morphotype in *H. crassidens*. See figure 1 for details and sample sizes. (Online version in colour.)

We therefore genotyped $n = 285$ offspring (i.e. 267 hatchlings plus 18 eggs) of which $n = 273$ were genotyped at three or more loci. We assigned paternity to 184 hatchlings/eggs. About 51 males sired offspring while 34 did not.

As predicted, male morphs did not differ in their average relative fitnesses ($\chi^2 = 3.96$, d.f. = 2, $p = 0.138$; figure 2).

Our linear mixed model (with female ID entered as a random effect) showed that 8th instar males sire a significantly greater mean (\pm s.e.) proportion of offspring per brood ($\bar{x} = 0.65 \pm 0.06$, $n = 20$) than 10th instar males ($\bar{x} = 0.31 \pm 0.10$, $n = 9$; $t = -3.1$, $p < 0.01$) but not more than 9th instar males ($\bar{x} = 0.48 \pm 0.06$, $n = 11$; $t = -1.6$, $p = 0.1$). The 9th instar males sire a similar proportion of offspring per brood as 10th instar males ($t = 1.6$, $p = 0.1$). This finding partially supports the hypothesis that smaller morphs overcome their lack of harem success to accrue fitnesses equal to 10th instar males via post-copulatory processes (e.g. sperm competition).

As predicted, the proportion of offspring produced by each morphotype was similar to its frequency in the population ($\chi^2 = 1.3$, d.f. = 2, $p = 0.509$; figure 3). Further, the proportion of offspring sired per morph (red dots in figure 3) fell within the appropriate morph-specific 95% confidence interval (figure 3).

4. Discussion

Our study of wild-caught Wellington tree wētā revealed that this species' three male morphotypes have equal fitness. This finding is inconsistent with a condition-dependent developmental strategy wherein unconventional males have lower fitness than conventional males because their poor condition and competitive inferiority results in them 'making the best of a bad job' and accruing some, but not equal, fitness [2,11,21,23]. Moreover, the results of common-garden studies showing that laboratory-reared male hatchlings mature at different instars despite being fed identical diets, and thus in

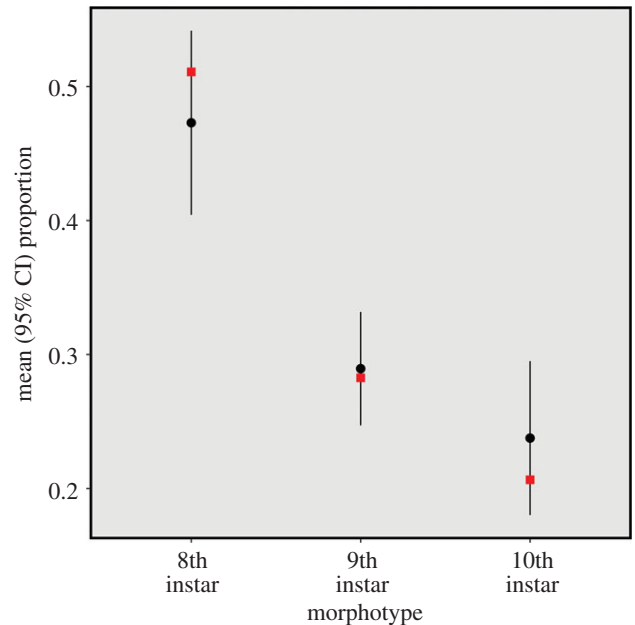


Figure 3. Mean (\pm 95% confidence interval) frequency ($n = 8$ years) of each morphotype on Maud Island (black dots and bars). The red squares represent the proportion of offspring produced by each morphotype in this study. (Online version in colour.)

similar condition, is also inconsistent with morph determination being condition-dependent in this species [40] (C.D.K. 2017, unpublished data). Instead, our results suggest that male *H. crassidens* morphotypes are part of a Mendelian strategy wherein each morph is genetically distinct [2,11,21]. To our knowledge, this study is the first example of alternative mating strategies being maintained by equal fitness in a wild population of insects. Only a handful of studies have supported the genetic polymorphism hypothesis [12–17] and even fewer have used molecular paternity assignment to directly quantify the reproductive success of alternative morphs in nature [48].

The natural history of Wellington tree wētā—obligately refuging in tree cavities during the day—uniquely permits sampling of all individuals competing for mating opportunities in a local area (i.e. a tree or group of trees). We were thus not only able to assign paternity to current harm-holders but also to those males not presently residing with females. Importantly, however, our sampling protocol permitted the inclusion of unsuccessful males of all morphs in our analyses. As Shuster *et al.* [2,3,21] point out, exclusion of these so-called zero-class males will inflate the average fitnesses of each morph while underestimating their variances, thus giving the appearance of morph differences in fitness when in fact none exist. Indeed, Wade & Shuster [3] showed that the inclusion of zero-class males equalizes fitness among morphs in a number of species in which subordinate or unconventional males were suspected of being condition-dependent strategists 'making the best of a bad job'.

Male Wellington tree wētā morphs have equal relative reproductive success despite differing significantly in harem size. In line with previous research [38,39], 9th instar males had significantly greater harem success than 8th instar males but significantly less success than 10th instar males. These data strongly suggest that 8th and 9th instar males accrue fitness by stealing fertilizations from conventional males rather than investing in the sexually selected precopulatory

mechanisms (i.e. intrasexual combat using enlarged mandibles as weapons) of 10th instar males [33,45]. Two lines of evidence suggest that unconventional males compete with 10th instar males in sperm competitive games. First, female *H. crassidens* commonly mate with multiple males [45] and, as shown in the current study, 8th instar males sire a significantly larger proportion of offspring in a brood than 10th instar males. Second, 8th instar males produce ejaculates that are, on average, absolutely larger than those of 10th instar males despite having absolutely smaller testes [49]. Such ejaculate expenditure is a hallmark of sneak copulators that face high risks of sperm competition [50,51]. Further experimental study is required to determine whether females preferentially use the sperm of smaller morphs or whether ejaculate characteristics of smaller morphs confer a competitive advantage over larger morphs.

The outstanding question, however, is how do the unconventional morphs gain mating access to females given that they are rarely harem masters? We argue that 8th and 9th instar males probably use a variety of means that are not mutually exclusive to gain access to sexually receptive females. First, our research (see [45]) suggests that unconventional morphs infiltrate cavities defended by larger morphs and then sneak copulations. For example, that we found smaller morphs (i.e. 8th and 9th instar males) with a larger morph in five galleries in our cross-sectional sample, which suggests that smaller morphs do indeed sneak into the harems of larger morphs. Second, unconventional morphs might also invest mating effort into searching for females who are outside of galleries foraging or ovipositing, for example, and not defended by 10th instar males. That copulations observed outside of galleries rarely involve 10th instar males (C.D.K. 2017, personal observation) supports this hypothesis. However, despite tremendous variation among males in the distances that they travel through the forest at night [34,52], and a hint of behavioural consistency within morphs [53], it is not known whether morphs differ specifically in their mate-searching behaviour. Third, unconventional males might gain sole mating access to

females who reside in galleries having entrance holes that are too small to permit entrance by larger males [30].

Gross & Charnov's [10] life-history model predicts that when different alternative strategies have equal fitnesses, the equilibrium proportion of males representing each life history in a population must equal the proportion of offspring produced by that life history. That the proportion of offspring produced by each tree wētā morph is remarkably similar to their stable proportion in our study population supports this prediction.

Our study provides empirical support, and the only evidence in an insect to date, for the hypothesis that the alternative mating strategies in *H. crassidens* are maintained by equal fitness and likely represent a Mendelian strategy. Further study is required to not only identify the mechanism underlying differential morph expression but to also explain how the unconventional morphs achieve reproductive success on par with 10th instar males given their significantly poorer success in monopolizing harems.

Data accessibility. Analyses reported in this article can be reproduced using the data and code provided at the Open Science Framework: <https://osf.io/8vqp9/>.

Authors' contributions. S.E.N. developed microsatellite primers, collected field data, conducted statistical analyses, conducted genotyping and contributed to writing of manuscript. C.D.K. designed field experiment, conducted statistical analyses and contributed to writing of manuscript.

Competing interests. We declare we have no competing interests.

Funding. This study was financially supported by the Canada Research Chairs program, the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants program and ReNewZoo, a Collaborative Research and Training Experience (NSERC-CREATE) program.

Acknowledgements. We thank Frank Higgott and Susan Caldwell of the Department of Conservation of New Zealand for assistance on Maud Island as well as Corey Davis and David Coltman of the University of Alberta for assistance in developing microsatellite primers. We thank two anonymous reviewers for insightful comments and suggestions that significantly improved our manuscript.

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