The Relationship Between Resource Control, Association with Females and Male Weapon Size in a Male Dominance Insect

Clint D. Kelly
Department of Biology, University of Toronto at Mississauga, Mississauga, ON, Canada

Introduction

Resource-defence polygyny occurs when females require particular resources for breeding, feeding and/or refuge, and individual males control these materials, permitting female access to them in exchange for copulations (Emlen & Oring 1977; see Shuster & Wade 2003 for a new classification scheme). Several studies in diverse taxa (e.g. mammals, Carranza 1995; birds, Göransson et al. 1990; reptiles, Kwiatkowski & Sullivan 2002; insects, Miya-take 2002) have shown a positive correlation between attributes of the resource (or territory) and the number of sexually receptive females visiting the resource; however, exceptions to this positive relationship are known (e.g. Yasukawa 1981; Baird 1988).

Given the potential reproductive payoff to males of controlling resources deemed more valuable by sexually receptive females, these sites should host more intense male–male competition for their ownership. Consequently, males with greater resource-holding potential (RHP; Parker 1974) should control more valuable resources. This prediction is supported by observational (e.g. Wells 1977; Severinghaus et al. 1981; Tsubaki & Ono 1987) and experimental (e.g. Lindstrom 1988; Kvarnemo 1995) studies in the wild. However, I note that male RHP need not provide females with benefits, genetic or otherwise, and so need not indicate ‘male quality’ to females.

Although more valuable resources attract more females and males with greater RHP typically control more valuable resources, do such correlations
observed in the wild result in greater harem (number of adult females residing with an adult male) success for larger-RHP males? Some studies of resource-defending insects (Gwynne & Jamieson 1998; Kelly 2005) have addressed this issue by examining only the latter relationship (i.e. male RHP vs. harem success), but have assumed positive covariance in the other two relationships (i.e. resource value vs. harem size and male RHP vs. resource value) and, therefore, can only infer causation. For example, a positive relationship between male RHP and harem size does not establish whether females are choosing to associate with larger-RHP males or are choosing the resources held by larger-RHP males, or are settling randomly with males defending more resources encountering more females. On the contrary, if there is no correlation between male RHP and resource value or between harem size and resource value then we can be more confident in concluding that receptive females choose male phenotype over resource value.

Ideally, one should examine all three of the above said relationships concurrently in a single experimental study to control for factors known to influence a male’s tenure on a resource (operational sex ratio, Blanckenhorn et al. 2003; population demography: e.g. male density, Borgia 1980; McLain 1992; ecological factors: e.g. predation risk, Gwynne & O’Neill 1980; individual state: e.g. energy levels, Marden & Waage 1990; Plaistow & Siva-Jothy 1996; environmental factors: e.g. temperature, Switzer 2002). Although some correlative (Howard 1978; Severinghaus et al. 1981; Tsubaki & Ono 1987; Villalobos & Shelly 1991) and experimental (Lindstrom 1988) field studies have examined the three relationships concurrently, these studies could not fully control the confounding factors listed above. Laboratory-controlled experiments are the best methods of combating these problems; however, to date few have been conducted (e.g. Lindstrom 1992). The present study deals with confounding factors by using a laboratory-controlled design in which pairs of males of a harem polygynous insect, the male Wellington tree weta, *Hemideina crassidens* (Tettigonioidae: Anostostomatidae), were permitted to compete in cages for resources required by adult females. Hemideina are large, flightless, nocturnal orthopterans endemic to New Zealand (Gibbs 1998). Anostostomatids live as adults for approx. 1 yr and exhibit various forms of male weaponry including cephalic tusks (Field & Deans 2001), and, in tree weta, exaggerated mandibles (Barrett 1991; Spencer 1995; Koning & Jamieson 2001; Stringer & Cary 2001; Kelly 2005). The Wellington tree weta, *H. crassidens*, is sexually dimorphic (Hudson 1920; Kelly 2005) with only males showing a striking variation in head size and associated mandible (weapon) length (Fig. 1) (Kelly 2005). The observed variation in head

---

**Fig. 1:** Heads from dried specimens of adult male Wellington tree weta, *Hemideina crassidens*, showing the approximate mean head length of males with smaller weaponry (x ± SD: 17.66 ± 2.80 mm) at left, and males with larger weaponry (25.90 ± 2.56 mm) at right, used in the trials. Head length of males is allometrically related to body size (Kelly 2005). Scale bar = 10 mm.
size in the wild is likely due to males maturing at either the eighth, ninth or 10th instar (females mature at the 10th instar only) and there is a positive covariance between final instar number and head size (Spencer 1995). Selection on head size is thought to be intense because males use their mandibles in fights for control of cavities in trees (galleries) in which one to several adult females shelter during daylight hours (C. D. Kelly, unpubl. data). Galleries are used year-round by both sexes and act as mating sites in addition to refugia (Field & Sandlant 2001). A correlative study in the wild showed a positive association between male head size and harem size; therefore, larger headed males appear to have higher mating success (Kelly 2005). Observations in the wild showed that females will mate with more than one male (C.D. Kelly, pers. obs.), but nothing is known about the role of female mate choice in male reproductive success. However, controlled studies showed that females prefer to reside alone in a gallery, possibly because of the high costs of harassment by males (C. D. Kelly, unpubl. data). Therefore, males may favour larger galleries while females do not. Taken together, the available evidence suggests that H. crassidens has a male dominance polygynandrous mating system (sensu Shuster & Wade 2003).

Not only is there male–male competition for galleries in tree weta, but there can also be intense competition between the sexes for gallery space (Field & Sandlant 1983; Moller 1985). As dawn approaches, predation risk from visual hunters likely increases and weta move to shelter (Field & Sandlant 1983; Moller 1985) causing adult males, which are more aggressive than adult females, to evict residents (small males or adult females) from small (i.e. single occupant) galleries (C. D. Kelly, pers. obs.). Consequently, galleries in nature are expected to show diurnal occupancy by a single adult male with adult females distributing themselves according to the remaining space among the galleries. Furthermore, if there is variation in size among galleries within a location, then there should be variation in the number of females (harem size) residing in galleries because larger refuges are able to accommodate more females. Despite a female preference for residing in a gallery without males (C. D. Kelly, unpubl. data), the costs of remaining in the open (e.g. predation risk) likely outweigh those of residing in a male-occupied gallery (e.g. male harassment). Taken together, female aggregation in galleries should increase the opportunity for sexual selection on males (Darwin 1874; Emlen & Oring 1977; Shuster & Wade 2003). Male tree weta controlling galleries with several females have the potential for higher reproductive success because copulations occur within the gallery and at the gallery entrance (C. D. Kelly, unpubl. data). Therefore, male–male competition for larger galleries containing more females should be more intense and males with larger weapons should control them.

The previous observational field study (Kelly 2005) showing a positive correlation between male RHP and number of cohabiting adult females in H. crassidens (see Gwynne & Jamieson 1998; Jamieson 2002; Leinsnham & Jamieson 2004 for similar observations in H. maori) did not identify the causal mechanism driving this relationship. Here, I address causal mechanisms by allowing pairs of males that differ in relative RHP to compete for two galleries that varied in size and thus could potentially house different numbers of females (harem size). I tested the following predictions:

1. Galleries with a larger volume host significantly larger harems than galleries with a smaller volume. Female tree weta should form significantly larger aggregations in the large gallery and a single adult male should reside in each gallery.
2. Males with larger weaponry (i.e. longer mandibles) control galleries with the largest volume. Because female aggregations will generate intense competition among males for that gallery, male tree weta with the largest weaponry (and greater RHP) should win more contests for control of the large gallery. Moreover, males with smaller weapons should have a greater likelihood of winning when the RHP asymmetry between opponents is small.
3. Males with larger weaponry accrue larger harems. If prediction 2 is met, then males with larger mandibles should cohabit with more adult females. Moreover, when RHP asymmetry is large, males with larger weaponry should be more likely to reside with larger groups of females.

Methods

Experimental Set-Up and Animals

This experiment was conducted in the laboratory on Te Hoiere/Maud Island, New Zealand (41°02'S, 173°54'E) during Apr. and May 2002. Natural light cycle and constant temperatures were maintained in the laboratory (approx. 15°C).

I used six cages (each measuring 50 × 50 × 50 cm), constructed of a wooden frame covered...
with small-gauge wire mesh with a floor covering of 1 cm of vermiculite. I installed two artificial galleries, a smaller gallery that could accommodate a single adult tree weta (17.95 cm$^3$) and a large gallery that could accommodate three adult tree weta (53.84 cm$^3$; large gallery). Gallery sizes were based on measurements taken on natural galleries in the wild (C. D. Kelly, unpubl. data). Prior to each trial, the large and small galleries were each randomly assigned to two of the four corners in a cage.

On the night prior to the start of a trial, I collected all experimental animals from the wild and by using digital callipers (Mitutoyo Digimatic, Mitutoyo Canada Inc., Toronto, Ontario, Canada) measured, to the nearest 0.05 mm, the total head length of each male. To facilitate identification, I numbered each individual uniquely with a small plastic bee tag (E. H. Thorne Ltd, Market Rason, UK). Male pairs were randomly assigned to a trial and were not matched for head or body size. The mean ± SD percent difference in head length for the 16 male pairs was 30.94 ± 14.52% and the range was 4.09–46.41% (see Fig. 1). In each trial, males of a pair were categorized as either ‘small’ or ‘large’ based on head length. Head length is an excellent predictor of mandible length (weapon size; Pearson’s product moment correlation coefficient, r = 0.99, n = 353; Kelly 2005).

Experimental Protocol

In the laboratory, experimental cages were placed on the ground approx. 2 m apart. On the first night of each trial, I placed two adult males and two adult females into each of the six cages. Each trial was run for 3 d to provide males and females with sufficient opportunity to locate and inspect galleries, and to establish ownership and residency in them. Each day at dusk, I fed the weta with a small quantity of chopped carrot and I lightly misted the cage with water.

All pairs of experimental animals were chosen randomly and no animals were used in more than one trial. I conducted 16 trials, and therefore 32 males and 32 females were used in this experiment. Two individuals of each sex were used because this is the minimum number required to have female aggregates and to stimulate competition between males. The experimental design used in this study is biologically realistic because galleries of different sizes can occur near each other (e.g. on the same tree) in the wild (C. D. Kelly, pers. obs.) and males with different RHP often encounter each other at galleries (C. D. Kelly, unpubl. data).

At the conclusion of a trial, I opened each gallery, identified the occupants and recorded the number of females residing with each small and large male. The number of females residing with a male was defined as ‘harem success’. All experimental animals were subsequently released into the wild.

Data Analysis

Wilcoxon signed-ranks test was used for all paired-sample tests because data were not normally distributed and differences between factor levels were symmetrical about the median (Zar 1999). All statistical tests were one-tailed because all predictions were directional. In addition, I used binary logistic regression to test whether differences in RHP predicted ownership of the large gallery. All analyses were conducted using SPSS 11.0 for Mac OS X (SPSS Inc., Chicago, Illinois, USA).

Results

As predicted, stimulus females aggregated significantly more in large galleries: large galleries hosted more females ($\bar{x} = 2$, range = 0–2 females, n = 16 trials) than small galleries ($\bar{x} = 0.5$, range = 0–1, n = 16) (Wilcoxon signed-ranks test, $Z = 2.62$, $p = 0.0045$; Table 1). However, the observed harem sizes were significantly smaller than expected (expected harem size in large gallery per trial = 2 females; $Z = 2.89$, $p = 0.002$).

In line with the prediction that males with larger RHP control higher-quality resources, males with longer mandibles controlled large galleries significantly more often than males with smaller mandibles ($n = 12$ vs. 4; $\gamma^2 = 4.0$, df = 1, $p = 0.023$). I also predicted that the large-headed male of a pair would be more likely to win control of the large gallery as head size asymmetry (the absolute difference between opponents in head length) increased. However, contrary to this expectation, there was no relationship between head size asymmetry and the

<table>
<thead>
<tr>
<th>Table 1: Total number of females that smaller and larger males resided with</th>
<th>Male weapon size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gallery size</td>
<td>Smaller</td>
</tr>
<tr>
<td>Small</td>
<td>4</td>
</tr>
<tr>
<td>Large</td>
<td>7</td>
</tr>
<tr>
<td>No choice</td>
<td>0</td>
</tr>
</tbody>
</table>

The ‘no choice’ categories include females that were alone either inside (n = 4) or outside a gallery (n = 2).
likelihood of the male with larger mandibles winning control of the large gallery (binary logistic regression, Wald statistic \( \chi^2 = 0.364, \text{df} = 1, p = 0.546; \text{Fig. 2} \)). Thus, very small males, on occasions, were able to outcompete very large males for the control of the large gallery.

However, males with larger mandibles were more successful at residing with females in large galleries (Pearson’s \( \chi^2 = 23.45, \text{df} = 4, p < 0.0001; \) Table 1). Nevertheless, however, males with larger mandibles (\( \bar{x} = 1, \text{range} = 0–2 \) females) did not have significantly greater harem success overall than those with smaller mandibles (\( \bar{x} = 0, \text{range} = 0–2; Z = 1.03, p = 0.152, \text{effect size } r = 0.256, n = 16; \) see also Table 1). This result was due to males with smaller mandibles having better success in small galleries compared with larger males; in four cases, the smaller male resided with a female in the small gallery (Table 1). The cavity volume of small galleries was too small to accommodate both a male with a very long head length and an adult female; males that resided with females in small galleries (\( n = 4 \)) had a mean head length of 18.65 mm whereas those that did not (\( n = 28 \)) had a mean head length of 22.23 mm.

The prediction that the large-headed male of a pair would be more likely to reside with two females as head size asymmetry increased was refuted: there was no relationship between head size asymmetry and the likelihood that the male with larger mandibles would reside with a two-female harem (multinomial logistic regression, \( \chi^2 = 34.30, \text{df} = 30, p = 0.269 \)).

**Discussion**

My results experimentally demonstrated that, as predicted, large galleries house significantly larger harems of female *H. crassidens* than small galleries, and males with larger weaponry control large galleries significantly more often. Hence, it is not surprising that males with larger weapons had greater harem success in large galleries compared with their opponents. However, a field experiment on Maud Island suggests that males fight for control of harems and not galleries per se (C. D. Kelly, unpubl. data); the tenure of males residing alone in a large gallery did not differ, on average, from the tenure of single males in small galleries.

Notwithstanding the suggestion that males appear to fight for harems rather than galleries per se, the present study strongly supports Kelly’s (2005) hypothesis for the mechanism driving the positive correlation between male RHP and harem size observed in the wild: male–male competition for larger harems that reside in larger galleries. The alternative hypothesis of female choice for males with larger weaponry was not supported here because females appeared to actively avoid males in general (i.e. they often resided alone in galleries; see below) and the overall relationship between male RHP and harem size was weak.

Contrary to prediction, males with larger weaponry did not have significantly greater harem success than males with smaller weaponry, although the trend was positive in favour of larger males (\( \bar{x} = 1 \) vs. 0 females for larger and smaller males). The lower than expected level of harem success for larger males is consistent with the weak selection (positive but statistically non-significant partial regression coefficients) on weapon size observed in the field on Maud Island (C. D. Kelly, unpubl. data). However, the findings of the current study are not consistent with those of Kelly (2005) in which male RHP and harem size were significantly positively correlated. The effect size observed in the present study for the relationship between male RHP and harem success (\( r = 0.256 \)) was much smaller than that found in natural (\( r = 0.52, n = 29 \)) and artificial galleries (\( r = 0.33, n = 79 \)) in the wild on Maud Island (Kelly 2005). This discrepancy is not likely due to my experiment being unrepresentative of nature; harem sizes in the present study (\( \bar{x} = 1, \text{range} 0–2 \) were...
similar to those found in natural (\(\bar{x} = 0\), range 0–5) and artificial (\(\bar{x} = 1\), range 0–7) galleries in the wild on Maud Island. More likely, in the present study, the combination of small effect size and small sample size hampered detection of a statistical difference in harem success between male head-size categories. There are three possible reasons for the small effect size observed here.

First, smaller males controlled the large gallery in four of 16 trials. Winning control of large galleries represented the primary contribution to the harem success of smaller males (\(n = 7\) females). Staged fights in the laboratory showed that male *H. crassidens* with smaller weaponry were occasionally able to defeat larger males in contests over galleries, but only when the relative difference in RHP between the opponents was small (C. D. Kelly, unpubl. data). However, such was not the case in this experiment as the victorious smaller males sported much smaller weaponry than the defeated larger male (Fig. 2).

Alternatively, perhaps in the four trials in which males with smaller weapons owned the large gallery, the male with smaller weaponry took up residence only after the male with larger weaponry deserted. In the wild, male *H. crassidens* exhibit a short duration of residency in galleries (\(\bar{x} \pm SE, 1.74 \pm 0.10\) d) and their tenure is positively correlated with harem size (C. D. Kelly, unpubl. data). That is, it appears that males take over galleries, mate with all resident females, leave the gallery and then roam in search of other female-occupied galleries. Thus, in the present study, the male possessing larger weaponry may have mated with the resident females and then left in search of other females.

Secondly, controlling the large gallery did not guarantee greater harem success as harem sizes were smaller than expected in large galleries. I expected two-female harems in each trial; however, this occurred in only seven of 16 trials. Smaller-than-expected harem sizes could have been due to a female preference for residing alone in galleries (C. D. Kelly, unpubl. data). Females were alone in the small gallery in four trials (not including the four trials in which a female was in the small gallery with a male) and stayed outside the gallery twice. These data provide further support (see C. D. Kelly, unpubl. data) that larger galleries are likely favoured by male *H. crassidens*. Moreover, that females could outcompete males for gallery space (\(n = 4\) females alone in small gallery) was unexpected; however, females did not outcompete males with very large weaponry (i.e. males with head length >23 mm).

Alternatively, smaller-than-expected harem success by larger-RHP males could have been the result of post-insemination aggression by males towards females (C. D. Kelly, unpubl. data). When a male encounters a female in a gallery, it will often extract the female from the gallery by grasping its hind legs its his jaws and pulling it out. Once the female genitalia are exposed, the male will attempt to copulate. After a successful copulation, the female will attempt to leave or re-enter the cavity, at this time the male will typically grasp the female in its jaws and throw the female from the tree (C. D. Kelly, unpubl. data). Therefore, the observed paucity of females in large galleries could be the result of the resident male mating a female and subsequently denying it re-entry to the gallery. Consequently, the observed low harem success of large RHP males may be more apparent than real.

Finally, although males with larger weaponry had greater harem success in large galleries, males with smaller weapons increased their harem success (and undermined the larger male’s success) by residing with females in small galleries. That males with absolutely smaller weaponry were able to reside with females in small galleries was unexpected; males that resided with a female in the small gallery had head lengths of approx. <23 mm (i.e. small weaponry; Table 1). Although the sample size is small (\(n = 4\)), this observation indicates that males with shorter mandibles (eighth and ninth instar adults) may gain access to females in galleries not accessible to larger males. This alternative mating scenario is plausible, given that small galleries (apparently single-occupant) are abundant in the wild (C. D. Kelly, pers. obs.).

In conclusion, the current experiment showed that larger males were better competitors for large-volume galleries (e.g. large galleries housing more females), but this did not guarantee monopolization of all available females; females may have exercised their preference for single-gallery occupation (by out competing males) and smaller males were often able to gain access to females in galleries too small to be accessible to larger males. Both factors should act to prevent larger males from attaining the upper limit to mating success.

Acknowledgements

I thank Darryl Gwynne, Stephen Shuster and an anonymous referee for comments on the manuscript. Steve Ward of the New Zealand Department of Conservation provided logistical support while this
work was conducted on Maud Island and Ian Miller (Department of Conservation, Nelson) kindly provided research permits. This study was supported by grants awarded to Darryl Gwynne from the Natural Sciences and Engineering Council of Canada and the National Geographic Society.

**Literature Cited**


