

Weak males do not work hard: Reproductive investment of deficient male fiddler crabs, *Austruca lactea*

Toshimasa Wakabayashi^{a,*} and Daisuke Muramatsu^{b,c}

^aNara University of Education, Takabatake-cho, Nara, 630-8528, Japan

^bCenter for Natural Environment Education, Nara University of Education, Takabatake-cho, Nara, 630-8528, Japan

^cWildlife Research Center, Kyoto University, 2-24 Sekiden, Tanaka, Sakyo, Kyoto 606-8203, Japan

*Corresponding author's e-mail address: wakabayashi.t.3@gmail.com

ORCID iDs: Wakabayashi: 0009-0003-0884-7783; Muramatsu: 0000-0001-8767-1488

Short title: Reproductive investment of deficient fiddler crabs

Abstract

In iteroparous animals, it may be adaptive to adjust the amount of reproductive investment based on their current competitive ability. Male fiddler crabs use an enlarged major claw for claw-waving display in the breeding season. Males sometimes lose their claws, but they can regenerate a claw, which is an inferior weapon for male-male fights. Here, we compared the waving frequency between males with a regenerated claw (regenerated males) and with an original claw (original males) to examine the differences in the amount of reproductive investment. Regenerated males showed lower waving frequency than original males, but some regenerate males waved frequently before the optimal mating season where original males waved frequently. These results indicate that individuals with poor fighting ability that have lower chance of acquiring females invested less in waving, and may also have shifted their peak of mating period in order to avoid competition with original males.

Keywords

reproductive investment, signalling, claw-waving, claw regeneration, alternative tactics, fiddler crab, *Austruca lactea*

1. Introduction

In species with multiple reproductive opportunities during their lifetime, it is not always adaptive to invest all one's energy in current reproduction, but rather to adjust the amount of reproductive investment according to one's relative competitive ability to maximise lifetime reproductive success (Kemp, 2006). High-quality individuals may breed in the optimal breeding season because they have a greater probability of acquiring mates at that time, whereas low-quality individuals may breed in the suboptimal season to avoid competing with high-quality rivals (Tina & Muramatsu, 2021).

Males of many species vary greatly in the expression of secondary sexual traits (Andersson, 1994). The discrete expression of secondary sexual traits has been considered to reflect alternative adaptations to heterogeneous social conditions (West-Eberhard, 1989). Social conditions permitting the coexistence of more than one phenotype may arise from differential competitive abilities of competing individuals

and the adoption of alternative reproductive behaviours (Gross, 1996). The expression of secondary sexual traits may cause changes in fighting ability and reproductive behaviour, which may affect their competitive ability (Moczek & Emlen, 2000). The beetle *Onthophagus taurus*, for example, shows a dimorphism for male horns: males that exceed a critical body size develop a pair of long, curved horns on their heads, while smaller males remain hornless (Moczek & Emlen, 2000). A horned phenotype is favoured in direct male–male competition and win females by expelling other males from their territory, while hornless males avoid physical contact with horned males (Siva-Jothy, 1987; Emlen, 1997) and mate with females by taking advantage of their manoeuvrability (Moczek & Emlen, 2000).

Males of fiddler crabs have a single enlarged major claw. The major claw is critical in territory defence and is a formidable weapon that is used in male-male fights (Jennions & Backwell, 1996; Backwell et al., 2007; Reaney et al., 2008; Lailvaux et al., 2009; Muramatsu & Koga, 2016), while the claw is also used for claw-waving display including ritualised contests and courtship displays (Muramatsu, 2011a, b; McLain & Pratt 2007; Muramatsu & Koga, 2016). The function of waving has been somewhat contentious, but is mainly considered to be used in courtship (e.g., Yamaguchi, 1983, 2001a; Burford et al., 2000; Pope, 2000a, b; Christy et al., 2001, 2002) and/or aggression (e.g., Crane, 1958; Salmon, 1965; Zeil et al., 2006).

Female choice in fiddler crabs is based on multiple male characteristics (waving frequency and major claw size; Reaney & Backwell, 2007) and multiple burrow characteristics (depth and temperature inside the burrow; Reaney & Backwell, 2007). Males of *Austruca lactea* have two types of mating tactics, burrow and surface matings (Yamaguchi, 1971, 1972, 2001a; Murai et al., 1987; Goshima & Murai, 1988). In burrow mating, males perform claw-waving and attract females into their burrows and copulations occur underground (Yamaguchi, 1971, 1972, 2001a; Murai et al., 1987; Goshima & Murai, 1988). In surface mating, male major claws play no special role, and males rarely perform claw-waving (Yamaguchi, 2001a); males visit females' burrows and copulate at the entrances to the females' burrows (Yamaguchi, 1971, 1972, 2001a; Murai et al., 1987; Goshima & Murai, 1988).

Males of *A. lactea* construct mud or sand structures (hoods) at the entrance to their burrows in the breeding season (Yamaguchi, 1971), to which they attract females for mating (Christy et al., 2001, 2003a, b). Hoods are thought to be traps that utilise the predation avoidance behaviour in females and attract females into their burrows (Christy et al., 2003a, b), while other males may perceive them as indicators of the resident male's potential fighting ability (Muramatsu, 2017). Because surface mating does not involve male burrows, hoods would not contribute to the mating success in surface mating (Muramatsu, 2010). Thus, hoods should only be constructed by males that invest in burrow mating.

Male fiddler crabs sometimes forced to autotomise their major claw during a predation attack, an escalated fight, or a problematic moult (Reaney et al. 2008), but they can regenerate a claw after the claw loss (Muramatsu & Koga, 2016). The regenerated claw is lighter, slenderer, and less robust than the original one (Figure 1) since regenerated claw contains less muscle mass and a thinner exoskeleton, becoming an inferior weapon for male–male fights (Backwell et al., 2000; Lailvaux et al., 2009; Bywater et al., 2014). Once males autotomise their claw, the shape of claws remains leptochelous (regenerated shape) (Yamaguchi, 1973; Rosenberg, 2002). Consequently,

males that have a regenerated claw (regenerated males) are weaker in male-male fights than males with an intact original claw (original males) in size-matched fights (Muramatsu & Koga, 2016).

Original males do not selectively fight against regenerated males; therefore, males may not be able to distinguish a regenerated claw from an original one (Reaney et al., 2008; Muramatsu & Koga, 2016) and regenerated claws may be effective bluffing tools in male-male contests (Backwell et al., 2000). However, the overall winning rate of regenerated males is lower than original males, even when the body size effect is taken into account (Muramatsu & Koga, 2016). As a result, regenerated males that have lost their burrows and are wandering tend to avoid fights with resident males, instead evicting females or searching for empty burrows (Reaney et al., 2008); therefore, the quality of their burrows may be lower than original males.

In the fiddler crab, a burrow and its surrounding area is a valuable resource used by both sexes as a refuge from predators, water supply, and foraging area (Callander et al., 2012a). In burrow mating, females mate inside the male's burrow and then use it as an incubation site (Backwell & Passmore, 1996). If the burrow collapses whilst the female is incubating, she could lose her entire reproductive investment (Reaney & Backwell, 2007). Burrow quality may also affect the incubation rate since the temperature inside the burrow varies with burrow size (Christy, 1987; deRivera, 2005). Therefore, females' final mate choice is strongly dependent on burrow quality (Reaney et al., 2008). In *Leptuca pugilator*, for example, females prefer stable burrows that are less likely to collapse during oviposition and incubation (Christy, 1983).

Male signals (waving frequency) positively correlate with key resource characteristics (the width and depth of the breeding burrow) in *Austruca lactea* (Tina & Muramatsu, 2022). By using the male signals, females may yield information about the burrows without entering the burrows. Females' final mate selection depends on male burrow quality (Backwell & Passmore, 1996); therefore, even if the male signals do not reflect the characteristics of their burrow, the female can reject the male after visiting the male burrows (Tina & Muramatsu, 2022). In such conditions, male signals are predicted to be honest because there is no reason for males to develop deceptive signals. This kind of honest signal is beneficial for both sexes; males can eliminate unnecessary investment in high-frequency waving, and females may be able to reduce the cost of entering and checking each male's burrow by using male signals (Tina & Muramatsu, 2022).

Regenerated males can fight on equal footing with original males when they have a 2.1-mm-longer claw than original males (Muramatsu & Koga, 2016). Therefore, when regenerated males grow up to be in the larger size class, they may be able to win contests and acquire high-quality burrows. Small and/or regenerated males may thus invest less in waving and hood construction for current reproduction, but invest more in body growth (including the major claw) for future reproduction. Alternatively, regenerated males may shift their mating period to avoid competing with original males. Indeed, small males of *A. perplexa* are inferior in fighting, not favoured by females, and shift their mating period to the suboptimal season (Tina & Muramatsu, 2021).

Under such conditions, crabs may manage their reproductive investment based on their relative competitive ability and avoid competition with high-quality rivals; however, the relative reproductive investment of original and regenerated males with

various body sizes have not been investigated. In the present study, we tested the two hypotheses: (1) whether small and/or regenerated males invest less in waving and hood construction, and (2) whether regenerated males shift the mating period to avoid the competition with original males. If crabs can finely manage their reproductive investment, small and/or regenerated males invest less under the presence of high-quality rivals.

2. Methods

2.1. Study site

All field observations were carried out in a dense colony of *Austruca lactea*, which was on an intertidal mudflat in the estuary of the Onosato river, Osaka, Japan (34°22'34"N, 135°15'04"E), during spring tides from May to September, 2023. Crabs emerged from their burrows and were active on the mudflat surface during the diurnal low tide. The entire study site was covered by the semidiurnal high tide, and the hoods constructed by the crabs were destroyed by the tide.

2.2. Study species

Austruca lactea inhabit sandy-mud tidal flats in estuaries or protected inner bays (Yamaguchi, 2000; Yamaguchi & Ogata, 2000). The annual growth of their carapace width reduces with the progress of growth, but there is no terminal moult; therefore, the age of crabs can roughly be predicted from their carapace widths (Yamaguchi, 2002). Males occasionally lose the major claw to predators or during an escalated contest (Muramatsu & Koga, 2016), and it takes approximately four months for the regenerated claw to recover to its original size (Yamaguchi, 1973). The relationship between carapace width and claw length are similar between original and regenerated males, and males cannot distinguish a regenerated claw from an original one (Muramatsu & Koga, 2016). However, human researchers can easily distinguish regenerated claws from original ones by the lack of large teeth in the gape of the claw (Yamaguchi 1973; Figure 1).

The breeding season of *A. lactea* is from early June to the end of August (Yamaguchi, 2001b) and vigorous claw-waving displays are observed during this period. Males of *A. lactea* are known to use four types of waving depending on the situation: (1) lateral-circular waving, (2) lateral-flick waving, (3) rapid-vertical waving, and (4) circular waving (Muramatsu, 2011a), of which lateral-circular waving and circular waving are thought to be related to courtship (Muramatsu, 2011b).

2.3. Waving frequency

A landmark (40-cm-long bamboo stick) was inserted 30 cm vertically into the sediment in the mudflat at the study site, and original and regenerative males close to the landmark were alternately observed with a video camera (HC-V360MS; Panasonic Holdings Corporation, Osaka, Japan) for 5 min each, and after the videotaping, the presence of hood (presence or absence) was documented. These hoods were newly constructed because all hoods were destroyed by semidiurnal high tides. The videotaped individuals were then collected, and the carapace width and claw length were measured with callipers to the nearest 0.05 mm. Crabs were marked by painting the number on their carapace for individual identification with a paint marker (MSR550P; Teranishi

Chemical Industry Co., Ltd., Osaka, Japan), and the paint surface was protected with cyanoacrylate adhesive (KS-4655; SHOEI Corporation, Osaka, Japan). To avoid pseudoreplication, the data were not taken from the same individual more than once. To exclude immature males from the analyses, males smaller than 10.0 mm were not used (Muramatsu, 2010).

To collect crabs, two steel sticks were used as tools. One end of the stick was placed beside the burrow entrance, and when crabs emerged from their burrows, the stick was moved to obstruct the burrow entrance (Muramatsu, 2010). Crabs were easily captured by hand after their way back into their burrows was blocked, because they always tried to retreat into their own burrow to hide and never attempted any other means of escape (Muramatsu, 2010).

2.4. The rate of hood construction

Five 1 m² quadrats at three-metre intervals, parallel to the Onosato river, were constructed and the number of male burrows was counted in each plot. Individuals emerging from the burrow were examined and the male's claw type and the presence of hood were recorded. Counting was conducted within two hours before and after the time of the lowest tide because most males complete hood construction at that time during spring tides (Yamaguchi et al., 2005). The time of the lowest tide was determined using the tide level forecast by the Japan Meteorological Agency (https://www.data.jma.go.jp/gmd/kaiyou/db/tide/suisan/s_kinki.php) as a reference.

2.5. Statistical analysis

To test the difference of carapace width and claw length between original and regenerated males, Student's t-test was applied using the 't.test' function in the statistical software R (R Core Team, 2021) after confirming the normality and homoscedasticity of carapace width and claw length using the Shapiro-Wilk normality test ('shapiro.test' function) and F test of homogeneity of variance ('var.test' function). If carapace width or claw length of original or regenerated males was significantly different from normal distribution, Wilcoxon rank sum test was applied using the 'wilcox.test' function.

To test the effects of male claw length, carapace width, claw type, the presence of hood, and the observation date on the frequency of male waving, the data were analysed using the Generalised linear model (GLM). The negative binomial distribution and log link function were applied to analyse the data, using the glm.nb function (Venables & Ripley, 2002) of the MASS package in the statistical software R (R Core Team 2021). The stroke number of lateral-circular waving and circular waving within the 5 min observation was selected as the response variable. The claw length, carapace width, claw type, presence of hood, observation date (categorical variable), and the interaction between claw type and date were fitted as the explanatory variables. The Akaike information criterion (AIC; Akaike, 1974) values for all possible models were calculated; the model with the lowest AIC value was considered to be the best model. Carapace width and major claw length were highly correlated in both original and regenerated males (Muramatsu & Koga, 2016); therefore, carapace width and claw length were not fitted in the same model to avoid multicollinearity.

To test the maximum waving frequency between original and regenerated males, the exact Wilcoxon signed rank test was applied using the exactRankTests package in

the statistical software R (R Core Team, 2021). The exact Wilcoxon signed rank test was also applied to test the differences of the hood construction rate between original and regenerated males.

3. Results

3.1. Carapace width and claw length

A total of 111 original males and 107 regenerated males were captured. The mean carapace widths of original and regenerated males were 13.30 (range: 10.3–18.2) and 13.75 (range: 10.1–18.1) mm, respectively. Regenerated males were significantly larger in carapace width than the original males (Student's t-test: $t = -2.48$, $p = 0.014$). The mean claw lengths of original and regenerated males were 19.08 (range: 13.4–27.0) and 20.78 (range: 11.4–29.4) mm, respectively. Regenerated males were significantly larger in claw length than the original males (Wilcoxon rank sum test: $W = 0.97$, $p = 0.008$).

3.2. Waving frequency

A total of 111 original males and 107 regenerated males were videotaped to count the waving frequency. The mean waving frequency was clearly different between original and regenerated males; original males showed a clear peak of waving at mid-July, while regenerated males did not have an apparent peak of waving (Figure 2). On average, regenerated males waved more frequently than original males in May to June, while original males waved more frequently than regenerated males in July and August (Figure 2).

In contrast to the mean waving frequency, the maximum waving frequencies of original and regenerated males within each observation day showed similar tendencies; both original and regenerated males waved frequently on 16th July and 2nd August (Figure 3). The carapace widths of original and regenerated males that showed the maximum waving frequency were 11.5 and 15.1 mm on 16th July, and 13.0 and 14.2 mm on 2nd August, respectively. The mean carapace widths of original and regenerated males were 12.5 (range: 10.3–13.9) mm and 13.0 (range: 11.1–15.2) mm on 16th July, and 13.8 (range: 12.1–15.9) mm and 13.4 (range: 10.5–14.9) mm on 2nd August, respectively. The claw lengths of original and regenerated males that showed the maximum waving frequency were 15.6 and 24.4 mm on July 16, and 19.4 and 22.1 mm on 2nd August, respectively. The mean claw lengths of original and regenerated males were 17.8 (range: 13.4–20.3) mm and 19.5 (range: 15.2–25.0) mm on 16th July, and 20.6 (range: 17.1–23.1) mm and 20.9 (range: 15.3–24.8) mm on 2nd August, respectively.

The results of the GLM analysis showed that claw length and carapace width strongly contributed to predicting waving frequency, and all top-10 smallest AIC models included claw length or carapace width as the explanatory variables (Table 1). In addition, the presence of hood, observation date, and claw type showed strong contribution because these model terms appeared frequently in high-ranked models (Table 1). From the rank 1 and rank 2 models, claw length contributed more to waving frequency than carapace width, but the difference of AIC values were negligible (Table 1). The best model contained four model terms: claw length, claw type, hood, and date (Table 1). The coefficient table of the best model showed that males with greater claw length, original type of claw, and hood waved more frequently (Table 2).

3.3. The rate of hood construction

A total of 492 original males and 135 regenerated males were observed within the quadrat during the observation. Original males constructed hoods more frequently than regenerated males (exact Wilcoxon signed-rank test: $V = 133$, $p = 0.038$).

4. Discussion

The data of the present study did not support our hypothesis that regenerate males shift their mating period; actually, their waving frequency did not show an apparent peak of waving. However, regenerated males waved more frequently than original males in May and June, suggesting that at least some regenerate males invested in waving before the optimal mating season. These regenerated males may have shifted their peak of mating period in order to avoid competition with original males. Consequently, mean waving frequency of regenerate males did not show an apparent peak of waving.

Unlike the mean waving frequency, the maximum waving frequency on each observation date did not largely differ between original and regenerated males; both original and regenerated males performed frequent waving on 16th July and 2nd August. Interestingly, the regenerated males that showed the maximum waving frequency were larger in carapace width and claw length within each observation date. These results suggest that high-quality regenerated males may have invested in waving at similar levels to original males in the same period of time. Regenerated males are weaker than original males in size-matched fights, however, they can fight as well as original males when they are sufficiently larger than the opponent (Muramatsu & Koga, 2016). Therefore, large regenerated males may be able to acquire and defend high-quality burrows, and thus waved frequently to advertise their burrow quality to females. By contrast, low-quality males that are less likely to be selected by females may invest less in waving, but invest more in body growth (including the major claw) for future reproduction. When regenerated males become larger than original males (especially when the regenerated claws become sufficiently longer), they will have more chances to defeat original males.

Another possibility is that regenerated males invest primarily in surface mating. Because waving and hood of *A. lactea* do not relate to surface mating (Yamaguchi, 2001a), investment in surface mating would not appear as the frequency of waving and hood construction. Therefore, we could not exclude the possibility that regenerated males invested in surface mating instead of saving energy for future reproduction.

Since the body size of *A. lactea* increases with age (Yamaguchi, 2002), the proportion of the regenerated males increases with body size because the probability of having regenerated claw (i.e. experiencing claw loss and claw regeneration) should increase with age. Indeed, both carapace width and claw length were significantly larger in regenerated males than original males in the present study. Because both waving frequency (Jennions & Backwell, 1998; Callander et al., 2012b; Zeil & Hemmi, 2006; but see Kim & Choe, 2003) and hood construction rate (Muramatsu, 2010) positively correlate with body size, it is difficult to argue that regenerated males have a lower waving frequency and/or hood construction rate without considering body size.

Because regenerated claws are lighter than the original claws of the same length (Backwell et al., 2000), the energy required for waving is likely to be lower in

regenerated males (How et al., 2009). In fact, however, original males waved more frequently than regenerated males. This counterintuitive result may be caused by the female choice based on burrow quality. Even if the regenerated males invest more in waving than the original males, they will not be selected by females unless the burrow quality is sufficiently high. Furthermore, unnaturally high-frequency waving for the given body size might be recognised by females that the signaller is a regenerated male.

In conclusion, regenerated males showed lower waving frequency and lower probability of hood construction than original males. Since regenerated males are predicted to have low-quality burrows (Reaney et al., 2008), they are less likely to be selected by females, which may consequently limit their mating investment. However, the mean waving frequency was higher in regenerated males than original males in May and June, suggesting that at least some regenerated males waved frequently before the period where original males waved frequently. In contrast, the maximum waving frequency on each observation date did not largely differ between original and regenerated males; therefore, high-quality regenerated males may have invested in waving at the level comparable to original males. Altogether, males of *Austruca lactea* finely manage their mating investment depending on their relative competitive ability. Similar tactics on the mating investment can evolve in other animals that have multiple reproductive opportunities during their lifetime. Further research, including interspecies comparisons, is thus needed to investigate what factors determine the amount of reproductive investment in individuals under various conditions.

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Table 1.

Values of the Akaike information criterion (AIC), ranked in increasing order, for generalised linear models explaining the frequency of male waving.

Rank	AIC	Model
1	2045.86	CL + CT + Hood + Date
2	2046.03	CW + CT + Hood + Date
3	2047.00	CL + CT + Hood + Date + CT:Date
4	2047.04	CW + CT + Hood + Date + CT:Date
5	2048.89	CL + Hood + Date
6	2048.90	CW + Hood + Date
7	2055.83	CL + CT + Date
8	2056.03	CW + CT + Date + CT:Date
9	2056.05	CW + CT
10	2056.13	CL + CT + Date + CT:Date

CL, CW, CT, Date, and Hood indicate claw length, carapace width, claw type (original/regenerated), observation date, and the presence of hood, respectively. ‘.’ indicates the interaction between the model terms, and ‘+’ indicates additional inclusion of the model term(s).

Table 2.

Maximum-likelihood estimates and their standard errors for each term in the best model explaining the frequency of male waving, selected based on the Akaike information criterion.

Model term	Estimate	SE
Intercept	-2.18	11.39
CL	0.26	0.54
CT (regenerated)	-6.90	3.15
Hood (presence)	18.64	5.46
Date (17 May)	5.17	8.16
Date (4 Jun.)	7.50	8.31
Date (17 Jun.)	18.81	7.76
Date (2 Jul.)	12.36	7.65
Date (16 Jul.)	30.91	7.83
Date (2 Aug.)	23.22	7.45
Date (16 Aug.)	11.69	7.60
Date (1 Sep.)	0.73	7.46

CL, CT, Hood, and Date indicate claw length, claw type (original/regenerated), observation date, and the presence of hood, respectively. Estimate indicates parameter estimates, and SE indicates standard errors.

Figure captions

Figure 1. Two types of claw shape in *Austruca lactea*. (a) males with an original claw, (b) males with a regenerated claw. Original claws have a robust shape and larger manus, and there are two large teeth in the gape of the claw; while regenerated claws have a slender shape and smaller manus, and lack the large teeth in the gape of the claw.

Figure 2. Relationships between the observation date and mean waving frequency (stroke/min) of original and regenerated males. Error bars represent the standard error of mean waving frequency of original and regenerated males, respectively. All observations were carried out during spring tides.

Figure 3. Relationships between the observation date and maximum waving frequency (stroke/min) of original and regenerated males. All observations were carried out during spring tides.



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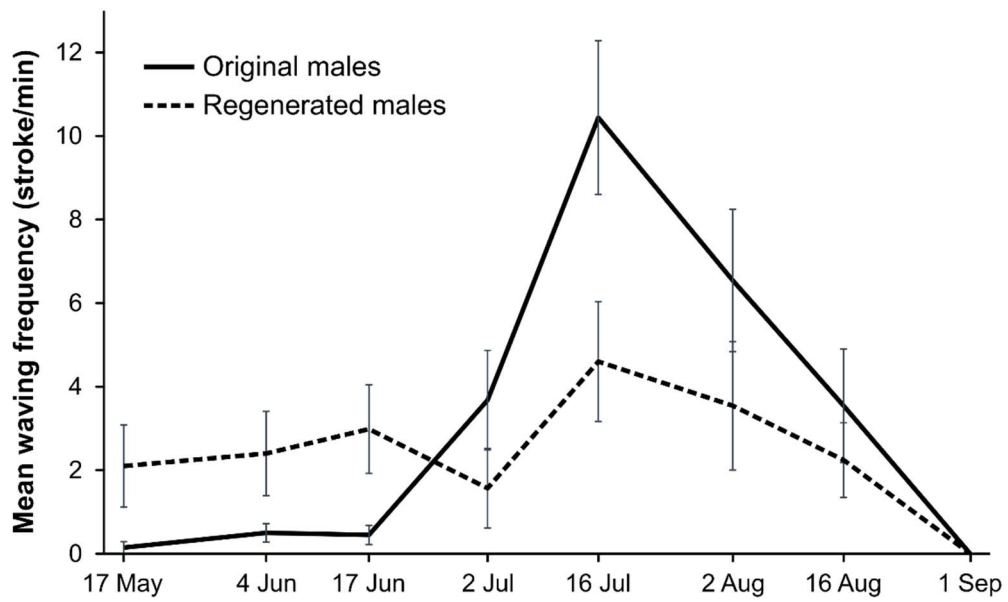


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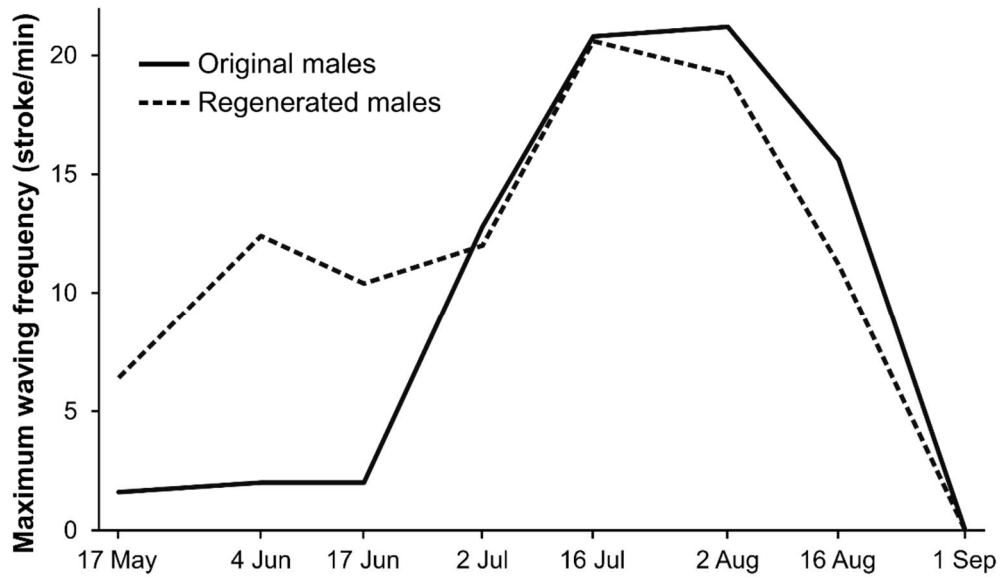


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