How and why the winner effect forms: influences of contest environment and species differences

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Winning aggressive social encounters can enhance the probability of future victories. This so-called winner effect occurs in diverse species and is thought to be an intrinsic phenomenon mediated by postconflict hormone release. Yet, recent evidence suggests the possibility that certain extrinsic factors also influence the winner effect’s formation within an individual, possibly by affecting the expression of hormone titters that follow a fight. We first investigated in the monogamous and territorial male California mouse (Peromyscus californicus) whether the effect of residency, an extrinsic factor, influences the winner effect’s formation and the endogenous secretion of testosterone and/or progesterone after a dispute. We found that California mice that acquire winning experience in unfamiliar physical locations do not form a full winner effect. Furthermore, this species does not experience a testosterone pulse after a fight in an unfamiliar cage. These findings indicate that environmental context can mediate the winner effect’s formation, possibly by affecting the expression of postconflict testosterone pulses. Second, we compared the winner effect of the California mouse to that of the white-footed mouse (Peromyscus leucopus), a close relative that is promiscuous and less-territorial. We found that, compared with California mice, white-footed mice exhibit neither a full winner effect, despite similar past winning experiences, nor a postconflict surge in testosterone. This finding suggests that these behavioral and physiological phenomena vary among even closely related species and are possibly linked to aspects of social biology, including the degree to which individuals of each species are territorial. Key words: aggression, Peromyscus, residency, social behavior, testosterone, winner effect.

In many animal species, past winning experience enhances the chances of future victories (reviewed in Hsu et al. 2006). Research indicates that this so-called winner effect can help to shape social structures and relationships, including the establishment of dominance hierarchies (Bergman et al. 2003; Dugatkin and Druen 2004) and possibly territorial interactions (Oyegbile and Marler 2006). Yet, despite the winner effect’s apparent functional relevance, little is understood about the processes that govern its formation within an individual on either a proximate or ultimate level.

In general, the winner effect is considered an intrinsic phenomenon, meaning that it is thought to form as the result of internal changes that transpire after a victory, including changes in perceived fighting ability (Beaugrand et al. 1991; Whitehouse 1997; Hsu and Wolf 1999) or actual fighting ability (Parker 1974). Although, a recent study found that individuals that accumulate multiple wins in their own territory showed a full winner effect when they fought future battles in that same territory, but showed a diminished winner effect when they fought future battles in an unfamiliar location (Fuxjager et al. 2009). This study illustrates that the environmental context of a fight can mediate the intrinsic properties that underlie the “expression” of a fully formed winner effect; this study does not address, however, whether the environmental context in which winning experience is accrued influences the “formation” of the winner effect in a given individual.

Physiologically, steroid hormones are thought to regulate the winner effect (Dugatkin 1997; Marler et al. 2005), particularly androgen hormones endogenously secreted after an aggressive social encounter (Gleason et al. 2009; Oliveira et al. 2009). Postconflict release of testosterone (T) is posited by the “Challenge Hypothesis” (Wingfield et al. 1990), and numerous studies, including some in humans, have confirmed that this phenomenon is taxonomically pervasive (see reviews by Archer 2006; Hirschenhauser and Oliveira 2006). Other steroid hormones, such as progesterone (P), that similarly mediate aggression (Kapusta 1998; Davis and Marler 2003; Weiss and Moore 2004) are also hypothesized to influence plasticity in winning ability (Davis and Marler 2003). Interestingly, research has indicated that the physical location or social context of a fight can influence an animal’s postconflict androgen responsiveness (Oliveira et al. 2005; Hirschenhauser et al. 2008; Fuxjager et al. 2009). This flexibility suggests a potential mechanism through which extrinsic factors might mediate the winner effect’s formation in a context-dependent manner (Oliveira et al. 2004; Gleason et al. 2009), although few studies have begun to consider and study this possibility.

Another element of the winner effect that remains elusive is the degree to which it and its underlying mechanisms vary among species, particularly among those that are closely related. Understanding this variation is important because it will likely provide a conceptual framework from which hypotheses can be generated to address the selective pressures responsible for the evolution of the winner effect. For example, the degree to which individuals of a given species are territorial might predict the presence of the winner effect because this enhancement in winning ability likely improves an individual’s competitiveness during aggressive encounters (Walls and Sемlisch 1991; Kemp 2000; Perry et al. 2004). The few

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Received 7 May 2009; revised 30 September 2009; accepted 3 October 2009.
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Behavioral Ecology
doi:10.1093/beheco/arp148
Advance Access publication 13 November 2009

Behavioral Ecology

California mouse (Peromyscus californicus), which is a monogamous and highly territorial species (Ribble and Salvioni 1990; Bester-Meredith et al. 1999; Gubernick and Teferi 2000; Trainor and Marler 2001; Oyegbile and Marler 2005). To address the second issue, we compared data obtained from California mice with those obtained from white-footed mice (Peromyscus leucopus), a close relative that is promiscuous and less territorial (Wolff et al. 1983; Wolff 1985, 1986; Wolff and Cicerello 1990; Xia and Millar 1991). We predicted that the winner effect’s formation in male California mice is influenced by residency status because this environmental factor can mediate the robustness of the winner effect’s expression (Fuxjager et al. 2009). Similarly, we predicted that in California mice the hormonal changes known to mediate the winner effect (i.e., postencounter T pulses) would occur only after fights in the home cage, as evidence indicates that residency influences postconflict physiological changes (Carre 2009; Fuxjager et al. 2009). In regard to the species comparison, we predicted that white-footed mice would show neither a robust winner effect nor a postencounter hormone release, which is significantly less territorial and aggressive (Wolff et al. 1983; Wolff 1986).

MATERIALS AND METHODS

Animals

California and white-footed mice were reared in laboratory colonies at the University of Wisconsin—Madison. Animals were maintained in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the appropriate institutional authorities at the University of Wisconsin—Madison approved of the research described herein. Each mouse colony was kept under a 14:10 h light-dark cycle (lights on: 03:00 CST). After weaning, individuals of the same sex were housed in the same-sex groups of 3 to 4 mice per cage (size: California mice- 48 × 27 × 16 cm; white-footed mice- 28 × 18 × 12 cm). California and white-footed mice were provided with Purina 5001 and 5015 mouse chow, respectively, and water ad libitum.

One week prior to the study’s onset, mice were transported into testing rooms. Both species were never held in the same testing room. To make observational work feasible for the experimenter, the 14:10 h light-dark cycle in each room was shifted so that lights went on at 22:00 CST (see Trainor et al. 2004; Oyegbile and Marler 2005, 2006; Fuxjager et al. 2009). Behavioral testing occurred during the dark phase under dim red light between 13:00 and 18:00. This study included 150 sexually naive male California mice, of which 46 were focal individuals, 60 were training intruders, and 44 were testing intruders. This study also included 57 sexually naive male white-footed mice, of which 24 were focal animals, 22 were training intruders, and 11 were testing intruders. All animals were between 6 and 13 months old.

Behavioral testing

To test if residency status influences the winner effect’s formation in California mice, we randomly assigned sexually naive male individuals to 1 of 4 different experimental conditions (Table 1, n = 11 per group): 1) three wins in the home cage followed by a test encounter in the home cage, 2) three wins in an unfamiliar cage followed by a test encounter in the home cage, 3) three wins in an unfamiliar cage and a test encounter in an unfamiliar cage, or 4) three handling experiences (i.e., no fights) in the home cage followed by a handling experience instead of a test encounter. Animals in the last group were used as hormonal controls, in that we collected blood from these individuals in order to provide baseline measurements of circulating hormones. Details regarding cage types and procedures are described below.

To test for species differences in the winner effect and postencounter hormone release, we randomly assigned white-footed mice to 1 of 2 experimental conditions (Table 1, n = 11 per group): 1) three wins in the home cage followed by a test in the home cage (identical to group one above) or 2) three handling experiences (i.e., no fights) followed by a handling experience instead of a test encounter. Again, mice that experienced only handling were used as hormonal controls.

On day 11, each pair was moved from a small standard cage (see dimensions above) to a larger, transparent Plexiglas cage (30 × 50 × 30 cm), which is referred to as the “home cage.” In each home cage, a transparent wall divided the inside space into 2 separate compartments (30 × 29 × 30 cm and 22 × 29 × 30 cm). Further, the dividing wall had 2 small openings at its base (5 cm diameter) that allowed mice to freely pass between compartments. For enrichment, a small wood nest-box was placed in the same location of each home cage. Mouse chow and water were also provided ad libitum.

Days 13, 15, and 17 consisted of the “training phase,” whereby focal individuals received either winning or handling experiences. Winning experience occurred in either the focal animal’s home cage or an unfamiliar cage, whereas handling experience always occurred in the focal animal’s home cage. Unfamiliar cages were constructed identically to home cages (described above) and, prior to their use, were washed thoroughly and lined with fresh aspen chip bedding so that they were completely unsoiled. Also, unfamiliar cages contained

<table>
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<tr>
<th>Table 1</th>
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<tr>
<td><strong>Six treatment groups to which male California and white-footed mice were randomly assigned</strong></td>
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<table>
<thead>
<tr>
<th>Species</th>
<th>Training phase</th>
<th>Testing phase</th>
</tr>
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<tbody>
<tr>
<td>California mouse</td>
<td>3 wins in HC</td>
<td>Encounter in HC</td>
</tr>
<tr>
<td></td>
<td>3 wins in UC</td>
<td>Encounter in UC</td>
</tr>
<tr>
<td></td>
<td>3 handles in HC</td>
<td>Handle in HC</td>
</tr>
<tr>
<td>White-footed mouse</td>
<td>3 wins in HC</td>
<td>Encounter in HC</td>
</tr>
<tr>
<td></td>
<td>3 handles in HC</td>
<td>Handle in HC</td>
</tr>
</tbody>
</table>

Handled individuals were used as controls for hormonal analysis.
food and a clean nest-box in the larger compartment, although the latter was placed in a different physical location within the unfamiliar cage compared with the home cage. Thus, unfamiliar cages differed from home cages in their scent and arrangement of objects within the cage. Focal mice neither experienced more than one fight in the same unfamiliar cage nor encountered the same nest-box during a fight.

Aggressive contests followed the resident–intruder (R-I) paradigm described previously (Trainor et al. 2004; Oyegbile and Marler 2005, 2006). For encounters in the home cage, the female was first removed and an opaque divider that blocked passage and sight between compartments was inserted into the cage. Focal individuals were kept in the cage’s larger compartment, and intruders were placed in the smaller compartment. The 2 individuals remained separated for 2 min so that the intruder had time to acclimate to its surroundings. The divider was then removed and the mice were permitted to interact for 10 min. For aggressive encounters in the unfamiliar cage, the R-I procedure was slightly modified, such that focal animals were removed from their home cage and placed into the unfamiliar cage’s larger compartment with the opaque divider already in place. The opponent was then placed in the adjacent compartment and allowed to acclimate for 2 min as described above.

The contest winner was defined as the individual that initiated at least 3 consecutive attacks (described below) that elicited either avoidance or freezing behavior (described below) from the opponent (Oyegbile and Marler 2005, 2006). Previous studies of Peromyscus behavior operationally defined winning behavior as initiating multiple attacks of biting, chasing, and wrestling, whereas losing behavior was defined as jumping away from an opponent, retreating, and freezing (Eisenberg 1961). To bias the training encounters so that focal individuals always won and therefore received the proper treatment, training intruders were sexually inexperienced, smaller, and losers of prior encounters (Trainor et al. 2004; Oyegbile and Marler 2005). Each training intruder was randomly assigned to its focal mouse opponent and never fought the same focal mouse more than once. Training intruders were used only twice for the entire experiment. Focal mice that did not clearly win all 3 of their training encounters were removed from the study (California mice: 5.5%; white-footed mice: 55%).

Focal individuals that experienced handling instead of an aggressive encounter experienced the same treatment imparted by the experimenter and the R-I paradigm; however, an intruder was never placed in the home cage. As such, when the opaque divider was lifted, the focal mouse did not have any behavioral interactions with a male conspecific.

On day 19, focal mice were subjected to a test encounter, in either their home cage or another unfamiliar cage (Table 1), which allowed for the assessment of the strength and magnitude of a winner effect (Oyegbile and Marler 2005, 2006). Test encounters followed the same R-I paradigms described above, except in this case the 10 min encounter was videotaped. Also, to reduce the effect of contest asymmetries among treatment groups during the test encounter, resources (i.e., nest-box and food) were removed from the home cages or were absent from unfamiliar cages. The probability of intruders winning in the test encounters was increased compared with training sessions because testing intruders were sexually experienced, slightly larger (mean ± standard error; 1.4 ± 0.22 g), and had won a single encounter on the previous day. In effect, this “intruder advantage” decreased the probability that focal mice randomly win their test encounter (~20%, see Oyegbile and Marler 2005) and therefore enhanced our ability to statistically detect a winner effect (Trainor et al. 2004; Oyegbile and Marler 2005, 2006). Test intruders were randomly assigned to focal mouse opponents and used only once.

**Behavioral analysis**

An observer blind to treatment groups analyzed the videotaped test encounters, scoring for each individual in a given test encounter the frequency of bites, chases, wrestling bouts (i.e., a stint of wrestling lasting at least 3 s), jumps away from the opponent, retreats from the opponent, and freezes (i.e., remaining completely still after initiating or receiving an attack). The observer also recorded each mouse’s attack latency (i.e., time between the encounter’s onset and an individual’s first attack toward its opponent). Finally, the observer calculated for all individuals the total attacks directed toward the opponent (i.e., sum of bites, chases, and wrestling bouts) and the total losing behavior elicited by the opponent (i.e., sum of jumps away, retreats, and freezes). Thus, the “total attacks” is a relative measure of an individual’s aggressiveness during the test encounter, whereas the “total losing behavior” is a relative measure of subordinate or losing behavior.

**Hormonal measurements**

Focal individuals were rapidly decapitated 45 min after the test encounter so that blood from the thoracic cavity (i.e., trunk blood) and the brain (used for another study) could be collected. Past studies indicated that this time point is when postencounter plasma T peaks in Peromyscus mice (Marler et al. 2005; Oyegbile and Marler 2005). Samples were immediately centrifuged and stored at −80°C until assayed. Hormone assays were conducted at the Wisconsin Regional Primate Center. Samples were extracted with ethyl ether, and steroids were separated using celite chromatography. All hormones were analyzed separately and in a manner described in detail previously (Bester-Meredith et al. 1999; Trainor and Marler 2001; Davis and Marler 2003). Briefly, T and P were analyzed separately using enzyme immunoassays (T antibody R156, University of California—Davis diluted to 1:35 000; P antibody R4861, University of California—Davis, diluted to 1:33 000). Corticosterone (Cort) samples were analyzed using radioimmunoassay (validated for California mice elsewhere [Bester-Meredith and Marler 2001]). The intra- and interassay coefficients of variation for each hormone measured, respectively, were as follows: T, 2.9% and 4.3% (n = 2 plates); P, 1.3% and 2.3% (n = 2 plates); and Cort, 0% and 3.1% (n = 1 assays).
Table 2
Aggressive behavior exhibited by focal individuals or their respective opponents during the test encounter

<table>
<thead>
<tr>
<th>Behavior</th>
<th>California mouse</th>
<th>White-footed mouse</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3 wins in HC; test in HC</td>
<td>3 wins in HC; test in HC</td>
</tr>
<tr>
<td>Attack latency (s)*</td>
<td>6.5 ± 2.5*a</td>
<td>8.8 ± 5.6*b</td>
</tr>
<tr>
<td>Total attacks*</td>
<td>65.0 ± 12.0*b</td>
<td>65.5 ± 7.4*a</td>
</tr>
<tr>
<td>Total opponent losing behavior*</td>
<td>39.0 ± 10.0*a</td>
<td>23.5 ± 4.1*a</td>
</tr>
</tbody>
</table>

Data are displayed as means ± standard error, but were natural log transformed for statistical analyses. “HC” means home cage and “UC” means unfamiliar cage. The asterisks adjacent to each behavior indicate an overall significant difference among treatment groups. Significant differences between values of a given behavior are indicated by differences in superscript letters.

Statistical analyses
Analyses were based on data obtained during the test encounters and from focal individuals, the one exception being analysis of losing behavior elicited from the opponents of focal mice. The relative differences in winning ability among treatment groups were analyzed with the Fisher’s Exact test modified for data arranged in a 2 × 4 table (Freeman and Halton 1951). Post hoc comparisons between treatment groups were conducted with the Fisher’s Exact test, using Holm’s procedure for multiple comparisons to control Type I error rate (Holm 1979). The Fisher’s Exact test was also used to compare the number of individuals of each species that were removed from the experiment during the training phase. Remaining behavioral and hormonal data were log transformed to meet conditions of normality (Zar 1999) and analyzed using SPSS 16.0 (Chicago, IL). We used a series of one-way ANOVAs to test if experimental treatments influence aggression and postencounter hormone levels, and post hoc analyses were conducted with Student-Newman-Keuls tests. We calculated Pearson’s correlation coefficients to test if any given behavior or hormone was correlated with postencounter T, P, or Cort (Zar 1999).

RESULTS
Winner effect
The physical location in which California mice acquired winning experience significantly influenced an individual’s ability to form a full and robust winner effect (Figure 1; P < 0.005). Analyses showed that California mice that acquire wins in an unfamiliar cage, regardless of the test encounter’s location, showed a diminished winner effect compared with California mice that acquire prior winning experience in the home cage (Figure 1; California mouse HC;HC vs. UC;HC: P < 0.004, California mouse HC;HC vs. UC;UC: P < 0.004). Furthermore, white-footed mice with past winning experience in the home cage also showed a diminished winner effect compared with California mice that acquired wins and a test encounter in the home cage (Figure 1; California mouse HC;HC vs. white-footed mouse HC;HC: P = 0.0125). As such, white-footed mice were behaviorally more similar to California mice that had winning experiences in unfamiliar cages, as there were not significant differences between these groups (Figure 1; all comparisons P = 1.0).

Additional analyses demonstrated that significantly fewer white-footed mice (11 of 24, ~45%) were able to win the 3 consecutive training encounters compared with California mice (33 of 35, ~95%) (P < 0.005).

Aggressive behavior
The physical location in which both the prior wins and the test encounter occurred significantly affected the level of aggressive behavior focal mice displayed toward their opponents and the degree of losing behavior focal mice elicited from their opponents (Table 2; attack latency: F_{4,37} = 2.94, P < 0.05; total number of attacks: F_{4,37} = 13.94, P < 0.01; total number of opponent losing behaviors: F_{4,36} = 8.44, P < 0.01). For attack latency, there were no significant contrasts among any given treatment groups. In regard to total attacks, California and white-footed mice that had winning experience and were tested in the home cage attacked opponents more than individuals that acquired winning experience in an unfamiliar cage (Table 2; California mouse HC;HC vs. UC;HC: q = 4.16, P < 0.05; California mouse HC;HC vs. UC;UC: q = 9.22, P < 0.01; white-footed mouse HC;HC vs. UC;UC: q = 10.61, P < 0.01; Table 2; white-footed mouse HC;HC vs. UC;HC: q = 5.56, P = 0.01). California mice that acquired winning experience in an unfamiliar cage but had a test encounter in the home cage attacked opponents more than those individuals that both acquired wins and had a test encounter in an unfamiliar cage (Table 2; UC;HC vs. UC;UC: q = 5.05, P < 0.05). Lastly, regarding opponent losing behavior, California and white-footed mice that both acquired wins and were tested in the home cage elicited more losing behavior from their opponents than individuals in the other treatment groups (Table 2; California mouse HC;HC vs. UC;HC: q = 5.23, P < 0.01; California mouse HC;HC vs. UC;UC: q = 3.99, P < 0.05; white-footed mouse HC;HC vs. UC;HC: q = 4.94, P < 0.01; white-footed mouse HC;HC vs. UC;UC: q = 3.75, P < 0.05).

Hormones
Analyses show that the physical location in which a test encounter takes place affects circulating T after the fight (Figure 2A; F_{4,36} = 3.00, P < 0.01). Post hoc tests revealed that California mice fighting a test encounter in the home cage, regardless of the location in which prior wins were accrued, had significantly higher plasma T 45 min after the dispute compared with baseline levels (Figure 2A, California mice only; HC;HC vs. Handled Control: q = 4.10, P < 0.05; UC;HC vs. Handled Controls: q = 5.49, P < 0.01). Furthermore, California mice experiencing a test encounter in an unfamiliar cage did not show a detectable difference in postencounter plasma T compared with baseline (Figure 2A, California mice only; UC;UC vs. Handled Controls: q = 0.97, P > 0.90). Unlike California mice, postencounter plasma T in white-footed mice fighting in the home cage was not different from this species’ basal level (Figure 2A, white-footed mice only; HC;HC vs. Handled Controls: q = 3.26, P = 0.075).
Correlations

In both California and white-footed mice, there was no significant correlation between any given behavior and T, P, or Cort (Table 3). However, in California mice, there was a significant positive correlation between postencounter P and Cort levels (Table 4; \( r = 0.653, \text{ slope } = 0.43, P < 0.001 \)). We detected no other significant hormone–hormone correlations (Table 4).

DISCUSSION

In California mice, winning experience accrued in an unfamiliar physical location tempers the formation of a full and robust winner effect (i.e., enhanced ability to win aggressive contests following past victories, reviewed by Hsu et al. 2006). This result demonstrates that the physical environment in which individuals acquire wins can influence the formation of the winner effect. Furthermore, these findings are consistent with our physiological data showing that postencounter T pulses responsible for mediating the winner effect (Gleason et al. 2009; Oliveira et al. 2009) are observed in California mice only after they fight in their familiar home cage. In contrast to the California mouse, the closely related white-footed mouse does not show a robust winner effect nor a postencounter T pulse, which might explain why this species does not exhibit a full winner effect.

Winning ability and aggressive behavior

In the territorial California mouse, the winner effect's full formation occurs only if past wins are acquired in a familiar home cage. Previous research showed that the winner effect is largely an intrinsic phenomenon, (Beacham 1988; Beaugrand et al. 1991, 1996; Whitehouse 1997; Hsu and Wolf 1999; Hsu et al. 2006), but our data are provocative because they suggest that these intrinsic properties can be governed by the environmental context in which winning experience occurs. Another experiment in California mice shows that the expression of an otherwise fully formed winner effect is similarly influenced by a fight's physical location (Fuxjager et al. 2009). Although it is possible that the effect of contest location interacts with an effect of social context to influence the winner effect, both the results from Fuxjager et al. (2009) and those presented here illustrate that contest location is a potent factor that influences both how the winner effect forms within an individual and how it is expressed in the future. To this end, our data illustrate an intriguing property of the winner effect that has not yet been described: it is likely bound to the environment in which it was formed. Studies in male crickets (Gryllus bimaculatus) have shown a similar phenomenon regarding plasticity in fighting behavior; namely, the depressed fighting ability a male cricket normally experiences after it loses a fight is muted once it engages in flight and presumably arrives at a different location (Hofmann and Stevenson 2000). Future studies should examine how long the winner effect lasts in an individual, particularly in territorial species since the dynamics that guide territoriality are flexible and, in some cases, change between breeding seasons (Vitousek et al. 2008).

The data presented here build further support for a connection between the winner effect and the residency effect, the latter of which is defined as an enhanced ability for territory owners to win contests that occur on their home range or territory (Krebs 1982; Waage 1988; Olsson and Shine 2000). Although the functional significance of this relationship requires more investigation, it is possible that the residency-dependent nature of the winner effect is related to territoriality (Oyegbile and Marler 2006; Fuxjager et al. 2009). For example, residency might be a cue that triggers the formation of the winner effect, such that an individual's ability to win aggressive contests is enhanced during instances of territory settlement or defense. At the same time, this mechanism presumably allows individuals to avoid investing energy into costly aggressive encounters that are unrelated to territoriality and therefore most likely offer fewer benefits associated with victory. Indeed, this interpretation is consistent with the comparative data present herein, in that the white-footed mouse, which is less territorial and wanders in search of potential mates (Wolff 1986; Wolff and Cicirello 1990), does not exhibit as robust of a winner effect as the highly territorial and monogamous California mouse (Ribble and Salvioni 1990; Oyegbile and Marler 2005). Furthermore, the observed species...
differences in the winner effect are not due to methodological biases (Hsu et al. 2006) because individuals of each species were examined in the same experiment and using the same protocol. Finally, although we hypothesize that territoriality and mating strategy are potential factors contributing to observed interspecific divergence in the winner effect, other factors might also influence this process. For example, in some species, the winner effect functions in part to help shape emerging social structures, such as dominance hierarchies (Dugatkin 1997; Bergman et al. 2003).

Our data also show that the level of aggressive behavior individuals exhibit during the test encounter varies among treatment groups and species, but not necessarily in the manner we might otherwise expect if aggressive behavior is always directly associated with winning ability. This is clearly demonstrated by our finding that California mice trained and tested in their home cage win more test encounters than white-footed mice with identical treatment and experience; however, focal animals in both groups do not show significant differences in either the total number of attacks directed at an opponent or the total number of losing behaviors elicited from an opponent. These data suggest that the winner effect is not reducible to simple changes in aggressive behavior that occur as a result of winning experience or fighting in a home cage. Instead, it is likely that other species-specific and dynamic properties between 2 individuals engaged in a fight underlie this behavioral phenomenon (Oliveira et al. 2009), which lends credence to the argument that the winner effect is an evolved adaptation rather than a by-product of regulatory processes guiding aggressive behavior (Rutte et al. 2006).

### Postencounter hormone levels

Postencounter T increases only after a fight in the home cage. Previous research suggested this possibility (Fuxjager et al. 2009), although this work showed neither that postencounter T “increased” relative to basal levels, nor that it was a response to the aggressive interaction itself. We experimentally addressed these limitations and showed that T does in fact increase after an aggressive social interaction in a context-specific manner. Furthermore, our results suggest that the expression of a postencounter T pulse is not strongly influenced by the location and context of past victories, implying that such experiences have little or no bearing on postencounter T responsiveness. However, this implication should be interpreted cautiously, not only because previous work has suggested that past winning experiences do in fact influence postconflict T responsiveness (Oyegbile and Marler 2005), but also because we cannot entirely rule out the effect of intrinsic factors on T responsiveness (i.e., males might adjust postencounter hormone responses with respect to future encounters or there might be an effect of a male’s ability to mount a postencounter T response). We also note that there are potential differences in the hormonal milieu and responsiveness between animals living in the laboratory and the field (Calisi and

<table>
<thead>
<tr>
<th>Species</th>
<th>Correlated variables</th>
<th>Correlation coefficient (r)</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>California mouse</td>
<td>Testosterone versus progesterone</td>
<td>0.314</td>
<td>0.076</td>
</tr>
<tr>
<td></td>
<td>Testosterone versus corticosterone</td>
<td>0.150</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Progesterone versus corticosterone</td>
<td>0.014</td>
<td>0.98</td>
</tr>
<tr>
<td>White-footed mouse</td>
<td>Testosterone versus progesterone</td>
<td>0.150</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>Testosterone versus corticosterone</td>
<td>0.006</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>Progesterone versus corticosterone</td>
<td>0.014</td>
<td>0.98</td>
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Asterisks (*) denote significant correlations (P < 0.05).
Bentley 2009), although a number of field and laboratory studies alike have demonstrated postcontest T pulses (Hirschenhauser et al. 2005; Hirschenhauser and Oliveira 2006). In regard to California mice, our data suggest an interesting caveat to the Challenge Hypothesis (Wingfield et al. 1990), in that contextual cues, such as a fight’s location, can help mediate within-individual variation in the expression of postencounter T pulses. Because this physiological phenomenon in part underlies the winner effect’s formation (Gleason et al. 2009; Oliveira et al. 2009), our data provide strong support for the hypothesis that environmental context can regulate the winner effect’s formation in a given individual by affecting steroid hormone action. Our findings join a larger body of work that shows that other factors, like the social context of a fight, similarly modulate expression of postencounter T pulses (Oliveira et al. 2001, 2005; Hirschenhauser et al. 2008) and therefore possibly also the winner effect (Oliveira 2004; Gleason et al. 2009). Other hypotheses propose that postencounter T helps regulate the persistence of territorial behavior (Wingfield 1994) and/or territorial site preferences in the wild (Marler et al. 2005; Gleason et al. 2009). Again, our findings are consistent with these different but nonmutually exclusive hypotheses, as the territorial California mouse, which demonstrates a clear winner effect, releases T after fights that are linked to territorial defense; whereas the less territorial white-footed mouse, which shows a weak winner effect, does not release T after disputes in the home cage. Other reasons might explain why white-footed mice do not show changes in postconflict T changes, such as the influence of mating system. For instance, phylogenetic analyses in birds have indicated that polygynous species show lower androgen responsiveness to aggressive social encounters compared with monogamous species (Wingfield et al. 1990, 2000; Hirschenhauser et al. 2003). Our results also conform to this pattern because white-footed mice mate with multiple partners (Xia and Millar 1991) and California mice demonstrate strict monogamy (Ribble and Salvioni 1990; Gubernick and Teferi 2000).

For both species, P levels did not change after aggressive contests in any of the treatment groups, limiting potential interpretation of P’s effect on aggression and winning ability. Recent work in diverse species, including California mice, has shown that P changes during or sometimes after aggressive encounters (Kapusta 1998; Davis and Marler 2003; Weiss and Moore 2004; Rubenstein and Wikelski 2005; Fuxjager et al. 2009). Yet, the role P plays in mediating aggression or winning ability remains elusive, in part because its effects vary substantially among species and between sex. For instance, in female rodents P can enhance aggression (Svare et al. 1986; Meisel and Sterner 1990), whereas in male rodents it can suppress aggression (Erpino and Chappelle 1971; Gravance et al. 2009). The issue becomes more complex considering that separate studies often use different techniques to stage aggressive interactions and therefore alter the contextual stimuli associated with a given contest. This is probably an important point when trying to understand how P regulates aggression, because this hormone is involved in mediating other physiological phenomena often associated with aggressive contests, such as anxiety (Schino 1998; Reddy et al. 2005; Schino et al. 2007). Furthermore, in California mice, there is a positive association between postencounter P and Cort. This indicates that adrenal glands might contribute to the postencounter P levels (Resko 1969) because this is the primary source of Cort secretions (Singer and Stack-Dunne 1955). To our knowledge, it is unknown whether the site of P release predicts its physiological function, although this adds to the interesting questions about P’s role in regulating aggressive behavior and winning ability.

Our results suggest that Cort does not change after an aggressive interaction in either species, even when that interaction occurs in a novel physical setting. Because Cort is often associated with increased stress (Nelson 2000), our data are consistent with the hypothesis that, at least in male California mice, aggressive encounters in a variety of contexts do not dramatically elevate physiological measures of stress.

Finally, the data presented here indicate species differences in basal steroid hormone levels. Compared with California mice, white-footed mice have lower basal levels of P and Cort, and probably higher basal T. The latter finding is a nonsignificant trend that has been statistically confirmed in a prior study (Marler et al. 2003). Hormonal mechanisms that serve as a physiological basis for life-histories traits are likely to be targets of natural selection (Hau 2007; Bokony et al. 2009); thus, it is not surprising that basal hormones differ between California and white-footed mice, because these species show different degrees of territoriality and strategies of acquiring mates. In regard to androgens, a phylogenetic analysis in Peromyscus mice of baseline T suggests that species differences are more likely to be related to ecological constraints imposed by the surrounding habitat rather than a given mating system (Marler et al. 2003). Certainly, this line of thinking agrees with additional analyses in birds that suggest that circulating hormones like Cort might be elevated in individuals when the risk of being stressed is both high and foreseeable (Romero 2002; Bokony et al. 2009). Yet, our results should be viewed in the context of broader phylogenetic analyses with caution because few experiments have been able to assess baseline hormones among a wide range of free-living mammals (Romero 2002), and differences in endocrine patterns might exist among vertebrate classes.

CONCLUSION

We show that extrinsic factors, namely the effect of residency status, influence the formation of the full winner effect in California mice. This process might occur as a result of extrinsic regulation of hormone release after an aggressive interaction, providing evidence for an interesting mechanism through which environmental stimuli can regulate plasticity in winning behavior in a context-specific manner. Furthermore, we show interspecific variation in the winner effect and its corresponding mechanisms, which might be due to species differences in territoriality and strategies used to acquire mates. This fact supports the notion that the winner effect is an evolved adaptation.

FUNDING

National Science Foundation Graduate Research Fellowship (to M.J.F.); National Science Foundation Grant (IOS-0620042 to C.A.M.).

We thank Jin Park and Andrea Charles for their assistance with the execution of the study. We thank Kyla Davidoff, Jan Davidoff, Katherine Cronin, Erin Gleason, Elizabeth Becker, and Josh Pultorak for helpful comments regarding the manuscript. We also thank Dan Wittwer and the Wisconsin Primate Research Center for conducting the hormone assays.

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