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Social context modulates how the winner effect restructures territorial behaviour in free-living woodpeckers

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Animal interactions such as competition are mediated by complex social strategies, which consist of behaviours and cognitive mechanisms that guide their production. As a result, behaviour is highly flexible. This poses a challenge to understanding how competition plays out in natural systems, because the course of a contest can essentially be rewritten by prior experience and/or changes in social context. Here we addressed this gap by studying how both of these factors interact to reconfigure competitive strategies used in territorial defence by a wild bird. After experimentally inducing the winner effect, a cognitive-behavioural phenomenon in which winning a contest increases the probability of winning again in the future, we found that male red-bellied woodpeckers, *Melanerpes carolinus*, adopted a new social strategy marked by more flexible transitions between different aggressive displays, as well as increasing overall aggressive output. However, this effect was mitigated by the arrival of the female social mate; in response to this momentary shift in social context, males decreased their use of territorial drum displays and became less likely to move around the territory or switch display modes during competition. In other words, the winner effect increased spatiotemporal diversity of territorial strategies, such that males frequently changed their location and display output. A female's arrival, however, reversed this effect. More specifically, males tended to revert to advertisement and social vocalizations on female arrival, which suggests that the need to attend to the social mate may supersede the threat of territorial intrusion. This is consistent with a model in which competitive outcomes are impacted by the interactive effects of an individual's past experiences and shifts in present-day social context, which may allow monogamous animals to effectively manage the competing demands of driving off intruders and attending to the social mate.

Animals live in a dynamic social environment, where a single behavioural repertoire must mediate different types of interactions. As a result, many behavioural phenotypes are both variable and flexible, changing dramatically in response to stimuli that operate on different timescales (Ghalambor, Angeloni, & Carroll, 2010; Miles, Vitousek, et al., 2018). This is facilitated in part by cognitive processes that allow animals to integrate both past experience and present-day social context into their behavioural decision making on a day-to-day basis (Hsu, Earley, & Wolf, 2006; Kemp & Wiklund, 2004). Understanding how these mechanisms function requires investigating how they operate in an ecologically relevant context. Work of this sort is rare, however, which poses a challenge to elucidating how behavioural flexibility shapes the outcome of animal interactions.

Competition is one commonplace interaction that influences the evolution of several behavioural phenotypes. In particular, behavioural signals (or displays) are critical for many species to negotiate competition, while avoiding the costs of an all-out fight (Bradbury & Vehrencamp, 2011). Unlike static signals, such as ornaments and weapons, display production is regulated by a complex suite of cognitive mechanisms that allow an individual to electively deploy behaviour in a context-appropriate manner. As a result, complex display repertoires evolve to meet the demands of both male–male competition and female mate choice (Miles & Fuxjager, 2018; Patricelli & Hebets, 2016), with individuals often shifting their behavioural output based on social environment (O'Loghlen & Rothstein, 2010; Schuppe, Sanin, & Fuxjager, 2016). For the most part, studies that examine behavioural flexibility and competition focus on changing display rates in response to various contextual stimuli (Delaney, Roberts, & Uetz, 2007; How, Hemmi, Zeil, &

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Peters, 2008). However, behavioural strategies also emerge when animals flexibly transition between different signals based on a variety of extrinsic factors (Egge, Brandt, & Swallow, 2011; Green & Patek, 2018; How, Zeil, & Hemmi, 2007). Such signal switching might provide a platform for individuals to temporarily modulate their aggressive response, without necessarily altering overall investment or output. If this is the case, then signal-switching strategies should be adaptive when aggression is costly in terms of its impact on individual condition, mating success or investment in parental care (Duckworth, 2006; Marler & Moore, 1988; O'Loghlen & Rothstein, 2010). Selection should therefore favour mechanisms that allow individuals to minimize these costs, while simultaneously increasing the probability of winning competitive interactions.

One such mechanism that may suit this role is the winner effect, a phenomenon defined as an increased ability to win aggressive contests after achieving social victories (Hsu et al., 2006). The winner effect has been reported in a variety of taxa, including arthropods (Whitehouse, 1997), fishes (Amorim & Almada, 2005; Dugatkin & Earley, 2004), birds (Drummond & Canales, 1998; Popp, 1988) and mammals (Fuxjager, Montgomery, & Marler, 2011; Oyegbile & Marler, 2005). Because it operates independently of an individual's intrinsic fighting ability, the winner effect can enable even poor competitors to achieve future victories given the right social experiences (Hsu et al., 2006; Oyegbile & Marler, 2005). Studies show that the formation and expression of the winner effect is highly dependent on contextual factors associated with a given contest, such as the familiarity of an opponent, the presence of bystanders and/or the physical location where the contest occurred (Apfelbeck, Stegherr, & Goymann, 2011; Fuxjager & Marler, 2010; Fuxjager, Mast, Becker, & Marler, 2009; Hirschenhauser, Gahr, & Goymann, 2013). This context sensitivity points to a compelling possibility that the winner effect acts as a behavioural rheostat, allowing animals to deploy either a high- or low-aggression strategy based on contextual demands. This is important because experience-induced behavioural changes can have profound consequences for social status (Dugatkin & Druen, 2004; Johnstone & Dugatkin, 2000). A context-sensitive winner effect may act as a force to swing behaviour between high and low extremes of aggressive output. In this sense, such an ability should be adaptive because it would allow individuals to reap the benefits of elevated aggression when it matters most, while avoiding the costs associated with aggression when it matters little (Fuxjager et al., 2011). This idea has seldom been studied, largely because the winner effect is predominantly measured in laboratory settings (cf. Apfelbeck et al., 2011) with little consideration about how it shapes the production of integrated territorial strategies.

Although the winner effect's flexibility in response to context cues has not often been explored in free-living animals, some studies highlight how social context reshapes behaviour in general. An individual defending its own territory, for example, is far more likely to win a dispute than if it fights in a neutral or unfamiliar location (Carré, Muir, Belanger, & Putnam, 2006; Jennions & Backwell, 1996; Kemp & Wiklund, 2004). At the same time, the presence of friendly individuals, such as pre-existing or potential social mates, can favour an entirely different strategy where antagonistic behaviour is less favourable (O'Loghlen & Rothstein, 2010; Patricelli, Coleman, & Borgia, 2006). Males may therefore have to adjust their behaviour when the sexes respond differently to displays; for instance, the wing-pumping display of a male cowbird, *Molothrus ater*, is effective in negotiating disputes between males, but may also drive off potential mates (O'Loghlen & Rothstein, 2010). At the same time, in socially monogamous species where both sexes defend the territory, both pair members will coordinate their behaviour more tightly in response to threatening intruders (Schuppe et al., 2016). The widespread and variable influence of a social mate's presence during competition suggests that this shift in context might shape how animals organize their strategic behavioural approach to competition.

Here, we explored this topic by investigating how repeated winning experience influences competitive strategies in wild red-bellied woodpeckers, *Melanerpes carolinus*. This cavity-nesting species is highly territorial during the breeding season, and it remains on this territory year round (Shackelford, Brown, & Conner, 2000). Both males and females are socially monogamous, each participating in parental care and typically maintaining a pair bond for multiple years. However, only male red-bellied woodpeckers defend the territory against conspecific intruders, and thus frequently engage in agonistic interactions across the breeding season (Kilham, 1961). In theory, forming a robust winner effect may help resident males modulate their aggression to efficiently negotiate these conflicts, since maintaining a relatively low level of territoriality until intrusions become a threat may be advantageous (Hsu et al., 2006). At the same time, however, males must also attend to their social mate, even during a territorial intrusion. Therefore, the social context set by a female's presence during this encounter (but not involvement in the encounter) might modulate how the male forms and expresses a winner effect.

We therefore tested the hypothesis that social experience and social context interact to shape the future behavioural strategies of resident male red-bellied woodpeckers. To do this, we exposed free-living males in a marked population to repeated simulated territorial intrusions (STIs) on consecutive days. By presenting playback and withdrawing it after a set period, we simulated the experience of winning a territorial contest for each encounter (Apfelbeck et al., 2011). After winning, we specifically predicted that males would begin to favour aggressive displays over prosocial signals, while also altering the spatiotemporal patterning of behaviour they produce in response to the intrusion. In approximately half of all encounters, females joined (observed) the simulations, thus shifting the social context of the dispute. If males do indeed have to attend to their social mate even during a territorial incursion, then this change in social context should mitigate the winner effect's drive towards elevated aggression. By assessing how males managed these competing demands in a high-stakes environment, we aimed to tease apart the tangled mechanisms that determine the course of competition.

METHODS

Study Species and Sites

We captured free-living male red-bellied woodpeckers (10 in the main group and four in the control group) using mist nets lured with conspecific playback between February and April 2017. A single net was deployed and observed continuously during the capture attempt, and individuals were extracted and processed immediately following capture. All captures were staged within 10 m of putative nesting or roosting sites, which we determined by the presence of an excavated cavity ca. 6 cm in diameter in semi-open deciduous forest or woodland. Once captured, each bird was individually marked for future identification with a unique randomly generated combination of three coloured bands and one federal metal band. We did not revisit any individuals within 14 days following the initial capture to ensure that individuals did not habituate to or avoid playback after being captured.

Experiments took place in April and May, which corresponds to the phase of peak territoriality for red-bellied woodpeckers, after a pair has selected a nest site but before any offspring have hatched (Shackelford et al., 2000). We terminated the study as soon as we first detected the presence of chicks in the study population (7 May 2017, determined via the presence of nestling calls and provisioning behaviour by parents). All fieldwork took place in forests and greenways throughout Forsyth County, NC, U.S.A. All procedures were approved via state and federal permit, as well as the Wake Forest University IACUC (Protocol no. A16-187).

Experimental Design

To examine how repeated winning experience influences future territorial behaviour, we staged a series of daily STIs over 4 consecutive days. STIs are widely used to elicit territorial behaviour in wild birds (e.g. Moseley, Lahti, & Podos, 2013; Nowicki, Searcy, Krueger, & Hughes, 2002; Schuppe et al., 2016; Searcy & Beecher, 2009; Wingfield & Lewis, 1993), and previous work suggests that the experience of undergoing an STI resembles that of winning a territorial contest (Apfelbeck et al., 2011). STIs were conducted between 0600 and 1100 hours, with trial start times determined at random for each individual on each day. STI stimuli were also chosen at random for each individual (see below for stimuli construction and validation), while taking care to prevent an individual receiving the same playback stimulus or trial time more than once. This not only avoids habituation to the stimulus, but also ensures that residents perceive 'intruders' as different (i.e. unfamiliar) individuals. The trials were designed to simulate the experience of winning for residents by presenting them with an aggressor that later 'retreated' after the resident bird responded. During each encounter, we recorded male behaviour and whether the individual responded alone or with a female (see Simulated Territorial Intrusions for more detail).

Other studies of the winner effect operationally define a win as having taken place when one individual attacks its opponent three or more times, with each attack eliciting losing behaviour (Fuxjager, Forbes-Lorman, et al., 2010; Fuxjager & Marler, 2010; Fuxjager et al., 2009; Oyegbile & Marler, 2005). However, in our current study using STIs in free-living individuals, residents did not have an opponent to directly attack per se. We therefore considered a win to occur when resident individuals produced three or more attack flights or drum displays, which red-bellied woodpeckers primarily use as directed agonistic signals (Kilham, 1961; Shackelford et al., 2000). This is feasible because red-bellied woodpeckers, like many other bird species, will respond just as aggressively to unseen playback from a conspecific as they will a visible intruder. Similar displays also precede rival displacement in woodpeckers and other birds, and thus are highly effective indicators that a social victory is taking place (e.g. Kilham, 1969; Popp, 1988). Therefore, by initiating playback, allowing a male to mount his territorial response and then withdrawing playback, we were able to simulate a comparable experience to a wild bird defending against an intruder that is not perched in the open (Apfelbeck et al., 2011). Conducting the experiment over 4 days allowed each male to accumulate 3 separate days of winning experience against unfamiliar individuals prior to examining resident agonistic behaviour on the fourth day's trial (which was conducted following the same protocol as all other trials).

Simulated Territorial Intrusions

Following previous playback studies using woodpeckers (Schuppe & Fuxjager, 2018; Schuppe et al., 2016), we conducted each STI within a 10 m radius of an individual's putative nesting/roosting site. Woodpeckers typically excavate a new cavity for nesting each year, but they are usually adjacent or very close to previous nesting or roosting cavities. Male red-bellied woodpeckers are most aggressive in their territory's 'core', which occupies a ca. 10 m radius surrounding their nest and/or roost (Shackelford et al., 2000). We therefore concealed a wireless speaker (JBL Model FLIP) mounted on a monopod 3 m up in a tree within this core area for each STI. To avoid habituating individuals to the speaker, we randomly selected a different tree for speaker placement on each trial day. No visual decoys, such as models or taxidermic mounts, were used during STIs, but this experimental set-up was nevertheless sufficient to elicit agonistic behaviour for all individuals on each trial day.

Each STI consisted of 10 min of playback made by looping one randomly selected set of stimuli. While broadcasting playback, we continuously recorded audio (same set-up as above). First, we noted each instance of key social behaviours typical for red-bellied woodpeckers: (1) 'churr' calls, (2) drum displays and (3) multifunctional social calls (rattle, 'chek' and 'woika' calls). The latter group pools multiple vocalizations that are less common and used by both males and females in uncertain contexts, so we grouped them separately from the territorial 'churr' calls and drum displays. We did not record 'displacement' comfort behaviours, such as preening and bill swiping, because they were rare (mode = 0 per trial). Finally, we noted attack flights made directly over the speaker, which were typically accompanied by an audible wing-rustling display (thought to be an aggressive signal in woodpeckers; Winkler, Christie, & Nurney, 1995). Because the wing-rustling sound was often too quiet to be detected by our recorder, we noted the occurrence of attack flights by hand and by dictation into the microphone. We also wrote and dictated each individual's time to first response (approach latency).

Finally, although male red-bellied woodpeckers are the primary territorial defenders in a pair (Kilham, 1961), we observed that females (presumably the social mate) often attended the STI without exhibiting overt aggression (i.e. we did not observe females producing 'churr' calls, drums or attack flights). As such, the female's role during the STI was that of an observer, rather than an active participant (a nontrivial distinction, considering that females of other woodpecker species do actively participate in territory defence against conspecifics; see Schuppe & Fuxjager, 2018). Although we did not have extra observers to track their behaviour, the presence of females was easily detectable because they typically made many flights from perch to perch in addition to producing nonaggressive social calls. We therefore noted which trials were joined by females to later assess how their presence influenced male behaviour in addition to simulated winning experience. Overall, female attendance appeared unpredictable and all individuals sampled underwent a mix of female absent/present trials on Days 1–3.

Acoustic Stimuli

Acoustic stimuli presented during the simulations were all constructed from the recordings of male red-bellied woodpeckers that we recorded with Tascam DR-100 Mk II recorder and Sennheiser SK-6 shotgun microphone (sampling rate = 44.1 kHz). We solicited acoustic signals with conspecific playback, which ensured that all acoustic stimuli contained directed displays, which can differ from spontaneous undirected signalling (ten Cate, 1985; Schuppe & Fuxjager, 2018). From these recordings, we created nine sets of acoustic stimuli modelled after the typical agonistic response. When individuals responded with acoustic displays, they primarily produced 'churr' calls (mean: 9.1 calls/min), followed by drumming (1.8 drums/min) and rattle calls (0.6 calls/min). Therefore, we based our stimuli on these three sounds by using a combination of 'churr' calls, drums and rattle calls in proportion with our observations. Each file contained signals from a single individual, and no signal was repeated across files.

We also ordered the presentation of signals based on our observation that all individuals ($N = 13$) recorded during this period responded first with vocalizations, with the majority ($N = 11$) first using ‘churr’ calls and two individuals responding first with nonaggressive social calls. ‘Churr’ calls were produced in chains of two to six separated by intervals of 0.6–1.2 s, while rattle calls and drums were deployed singly. After taking all of this into account, we designed the stimuli to begin with a string of ‘churr’ calls, with all following signals randomly ordered. Between each signal we added a 10–30 s pause to generate a 1.5 min stretch of active playback (final order: three ‘churrs’, one drum, one drum, two ‘churrs’, one drum, five ‘churrs’, one rattle, three ‘churrs’, one drum) with a final 30 s silent period to the end of each file.

Control Trials

To verify that our results reflected a response to repeated agonistic victories, rather than exposure to playback and observation, we also conducted a series of control trials on a separate sample of individuals ($N = 4$). Control trials followed the same protocol as experimental trials, but substituted heterospecific playback for red-bellied woodpecker stimuli. In each case, heterospecific playback was randomly selected from spontaneous recordings of local (non-woodpecker) birds singing (species included: *Turdus migratorius*, *Sialia sialis*, *Thryophorus ludovicianus*, *Toxostoma rufum* and *Pipilo erythrophthalmus*). We used these trials to verify whether male behaviour changed due to observation/playback alone. After the fourth day of heterospecific playback, we conducted a final STI on the following day where we instead presented the standard experimental (i.e. red-bellied woodpecker) stimuli as described above. We compared the results of these Day 5 control trials to Day 1 experimental trials; if observed behavioural shifts are the result of a winner effect, then this control trial should be similar to the Day 1 trials for experimental individuals. We tested this hypothesis using linear mixed models (LMM; see below).

Data Collection and Analysis

We first characterized aggressive response by counting ‘churr’ calls and drum displays performed during each STI, as these are the main acoustic signals used in territorial competition by red-bellied woodpeckers (Shackelford et al., 2000). Counts were conducted both in the field, where they were hand tallied by the primary field observer (M.C.M.) and counted post hoc from audio recordings by a different trained individual who was unaware of treatment conditions and experimental aims. This allowed us to quantify error and compare both methods for conducting behavioural counts (Appendix Fig. A1). The resulting counts were strongly correlated for both the number of drum displays ($R^2 = 0.96$, $P < 0.0001$) and ‘churr’ calls observed ($R^2 = 0.94$, $P < 0.0001$), and were thus also correlated for the sum of drum displays and ‘churr’ calls ($R^2 = 0.92$, $P < 0.0001$). All analyses of count data used the figures from the audio recordings for consistency, as our sequential data set was also derived from recordings.

We tested for differences in behavioural output using LMMs fitted via maximum likelihood in the R package ‘lme4’ (Bates, Maechler, Bolker, & Walker, 2015), where we modelled behaviour output, approach latency and minimum distance from speaker as a response to the fixed factors of trial day (Day 1 versus Day 4) and female presence (yes/no). Individual and stimulus identity were also included as random factors, and we accounted for differences in male response time by including time active as a covariate. Behavioural count data were cube-root transformed to achieve normality, and we log-transformed approach latency for the same reason. Finally, we corrected all P values to avoid spurious conclusions due to multiple testing (Holm, 1988) by using the ‘p.adjust’ function in base R.

To assess territorial strategy in terms of transitions between behaviours (independently of the volume of behavioural output), we next transcribed the full sequence of behaviours documented during each STI. In addition to drum displays and ‘churr’ calls (agonistic acoustic signals), the sequences also included attack flights and multifunctional social calls. Attack flights were verbally documented in real time on the same audio recording by a field observer, and thus could be positioned sequentially along with acoustic behaviour. In trials where a female was present, the field observer verbally distinguished when a call was performed by the female to ensure it was not counted (note that this category did not include the contact call ‘chek’, because it was not always possible to confidently attribute the call to a specific individual in trials where a female was present).

To analyse sequence data, we computed the number of transitions between behaviours for each trial. Because we tracked male flights during the trials, this approach allowed us to gauge how behaviours were patterned relative to one another across both space and time. To test whether individuals exhibited different transition patterning on Day 4, we used a chi-square test comparing our observed counts to a null distribution based on the proportional allocation of behaviour on Day 1. We used the same approach to test for an effect of female presence, this time testing whether the distribution of the transition matrix differed in female-present and female-absent trials. We again Holm adjusted P values for multiple testing.

Finally, behavioural strategies encompass not only what an animal is doing, but how behaviours are used across space and time. We first assessed whether winning experience predicted a shift in when males signalled the most during the trial. To do this, we calculated the proportion of displays produced during each 1 min interval relative to the total over all 10 min. In other words, each minute phase contained a proportion between 0 and 1 of the bird's overall aggressive behaviour, where values closer to 1 would indicate higher output relative to other minutes in the trial. To compare trials before a win (Day 1) and after a win (Day 4), we plotted signal proportion as a function of time in the trial for each group and then tested for differences using a two-way analysis of variance (trial day x minute).

RESULTS

Behavioural Output

We first examined how repeated victories against unfamiliar opponents influenced future territorial aggression. Males produced more aggressive displays overall after experiencing three simulated wins (Fig. 1a; $F_{1,9.9} = 15.12$, $P = 0.003$), an effect that appears to be primarily driven by increased output of territorial drum displays (Fig. 1b; $F_{1,10.5} = 11.77$, $P = 0.006$). There was no difference in the number of territorial/advertisement vocalizations (‘churr’ calls) used between Days 1 and 4 (Fig. 1c; $F_{1,11.7} = 2.12$, $P = 0.535$). These effects took place independent of male response time, as our statistical models included time active as a fixed factor and found that it did not predict output for any display (Appendix Table A1).

By contrast, we also found that the social context of the aggressive dispute influenced many of these effects. For instance, males produced fewer drum displays during trials with a female observer present (Fig. 1b; $F_{1,17.6} = 5.35$, $P = 0.033$), with no interaction between female presence and trial day (Fig. 1b; $F_{1,10.7} = 0.245$, $P = 0.631$). We did not find a similar attenuation of aggression in the presence of the female for other displays, as female presence did not predict a change in overall display output (Fig. 1a; $F_{1,17.2} = 2.75$, $P = 0.114$) or ‘churr’ vocalizations (Fig. 1c;

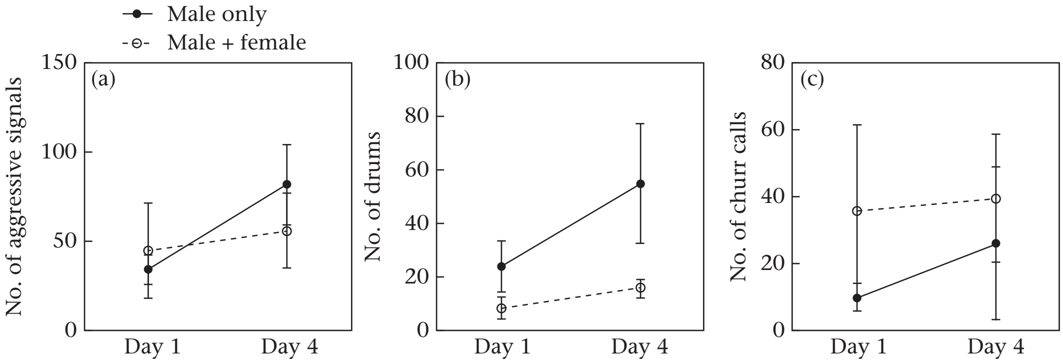

Figure 1. Mean (±1 SEM) counts of male red-bellied woodpecker displays performed during 10 min simulated territorial intrusions over 4 consecutive days, i.e. providing 3 days of simulated wins, when only the male respondent was present and when a female was also present.

$F_{1,10.1} = 0.265$, $P = 0.535$). In other words, the observed overall increase in aggressive display output appeared to take place independently of female presence.

Temporal Patterning of Territoriality

By tracking male approach dynamics and behavioural sequences (including attack flights), we were also able to assess territorial strategies as they took place across space and time (Fig. 2a). We first found that males responded to playback marginally faster (lower approach latency) by the fourth day ($F_{1,19} = 3.39$, $P = 0.081$), whereas female observation alone did not predict a change in approach latency ($F_{1,19} = 0.001$, $P = 0.970$). However, winning experience and female presence had a significant interaction on approach latency ($F_{1,19} = 5.51$, $P = 0.029$), where repeated wins drove males to approach faster only when they responded alone ($F_{1,2.1} = 191.7$, $P = 0.018$) and not when a female observer was present ($F_{1,6.7} = 0.645$, $P = 0.454$).

Because male approach times were highly variable, we then asked whether individuals concentrated their aggressive behaviour in a specific timeframe during the encounter (Fig. 2b). We discovered that, rather than shifting their behavioural output to a certain portion of the trial, males allocated their aggressive behaviour equally across each minute of the 10 min trial on both the first day ($F_{1,93} = 0.897$, $P = 0.346$) and after experiencing three wins ($F_{1,93} = 2.67$, $P = 0.109$). Thus, past experiences did not alter when male aggression was most robust during an encounter.

Control Trials

On average, aggressive responses to the conspecific playback were significantly elevated compared to heterospecific controls (Day 1 and Day 4) based on the number of drums ($F_{1,6} = 12.9$, $P = 0.011$) and ‘churr’ calls ($F_{1,6} = 0.033$), as well as both in combination ($F_{1,6} = 9.49$, $P = 0.022$). The one exception is approach latency, which was indistinguishable between trials ($F_{1,6} = 3.09$, $P = 0.139$). Importantly, Day 1 and Day 4 heterospecific trials were indistinguishable from each other (drums: $t = 1.10$, $P = 0.550$; ‘churr’ calls: $t = 1.07$, $P = 0.360$; total signals: $t = 1.51$, $P = 0.349$; approach latency: $t = 1.54$, $P = 0.351$).

When we compared resident bird responses to conspecific playback after they had heard the heterospecific controls (Day 5 in the control birds) to the experimental group's trial on Day 1, we found that these two groups were similar in terms of output for drums ($t = 2.48$, $P = 0.105$), ‘churr’ calls ($t = 1.47$, $P = 0.145$) and both signals combined ($t = 1.99$, $P = 0.156$), as well as approach latency ($t = 1.24$, $P = 0.482$).

Spatiotemporal Strategy

In a final analysis, we explored how experience and context shape the broader competitive strategies that resident males use to combat perceived rivals in a territorial bout. We therefore examined the transition probabilities between four key behaviours produced during these interactions: ‘churr’ calls, nonaggressive

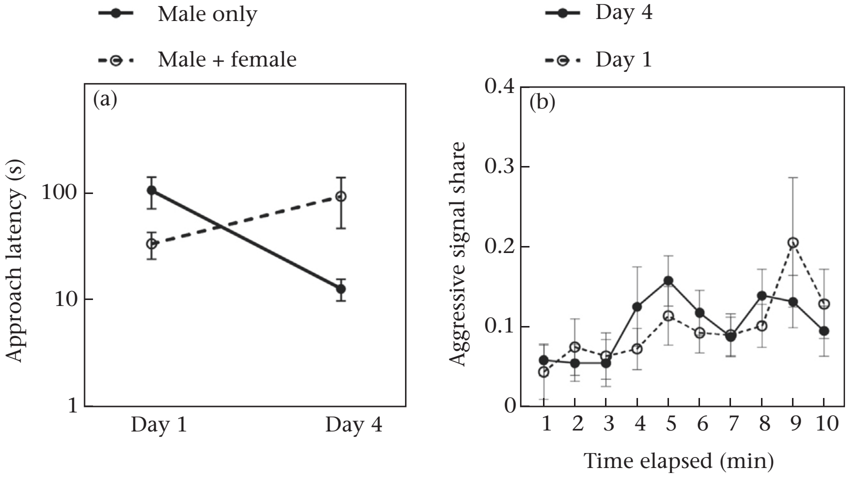

Figure 2. (a) Temporal dynamics of territorial behaviour in terms of male approach latency during territorial intrusion. (b) The proportion of total aggressive output in each minute of the trial. Values reported in (b) are averaged across trials with and without a female present as sample sizes were too small to examine each 1 min interval separately.

social calls, drum displays and attack flights (Fig. 3). When males responded to playback on the first day (no winning experience) without a female present (Fig. 3a), their most common first response was an attack flight over the speaker. Repeated flights were uncommon, and thus males typically transitioned into a state of repeatedly 'churr' calling or drumming. Only after these extended bouts of producing the same agonistic signal did males disrupt this pattern by flying to a different perch. In some cases, males would also transition from attack flights into the production of nonaggressive social calls, potentially signalling to their mate. However, resident males never transitioned from producing these social calls into a state of producing repeated aggressive displays (churr calls and/or drums).

After the males had accrued three wins, we found statistically significant changes in this behavioural transition network (Fig. 3b; male only: $\chi^2_6 = 13.0$, $P = 0.037$; all trials: $\chi^2_6 = 151.83$, $P = 0.003$). Thus, in the new strategy, we found evidence for more frequent transitions among territorial 'churr' calls, drum displays and attack flights after winning. This means that males now produced repeated bouts of aggressive churr calls before immediately transitioning into drumming behaviour (and vice versa), whereas this did not occur without prior experience. Moreover, male transitions into states of nonaggressive social calling completely disappeared.

Social context has equally profound effects on male competitive strategies. We found that, if a female was present on the first day, the transition network of male behaviours was significantly different from Day 1 trials without a female observer (Fig. 3c; $\chi^2_6 = 112.6$, $P = 0.003$). Specifically, males overwhelmingly responded first with a 'churr' call, while continuing to vocalize throughout the trial with almost no transitions into attack flights or drum displays (Fig. 3c). In rare cases, males immediately transitioned into an attack flight, followed by a transition into other behaviours (drumming and nonaggressive social calls).

At the same time, we found that the presence of a female influenced the changes to competitive strategy that past winning experience induced (Fig. 3d; male + female: $\chi^2_6 = 103.2$, $P = 0.003$). Specifically, males initiated the encounter with either multifunctional 'churr' calls or nonaggressive social calling. Only through either of these calling states did males transition into other behavioural traits, such as attack flights and drumming. The higher transition rates between different agonistic signals were still present in Day 4 trials when a female was present, which we also found in Day 4 trials when males responded alone. In this way, experience appears to underlie the production of a more diverse and complex strategy independent of social context. Yet, despite this similarity, we still found that the Day 4 strategy with a female observer was significantly different to Day 4 trials with only males ($\chi^2_6 = 402.5$, $P = 0.003$).

DISCUSSION

Our findings suggest that the winner effect acts as a mechanism for free-living animals to functionally enhance multiple facets of their territorial defence strategies during the breeding season. First, we found that winning experience predicted an increase in male red-bellied woodpeckers' future behavioural output, specifically with respect to drum displays that play an important role in territorial competition (Miles, Schuppe, Ligon, & Fuxjager, 2018; Schuppe & Fuxjager, 2018). Moreover, males were faster to respond to playback after experiencing repeated wins (provided they were not attended by a female observer). By contrast, males exposed to heterospecific control playback showed no change in aggressive behaviour with repeated encounters and behaved

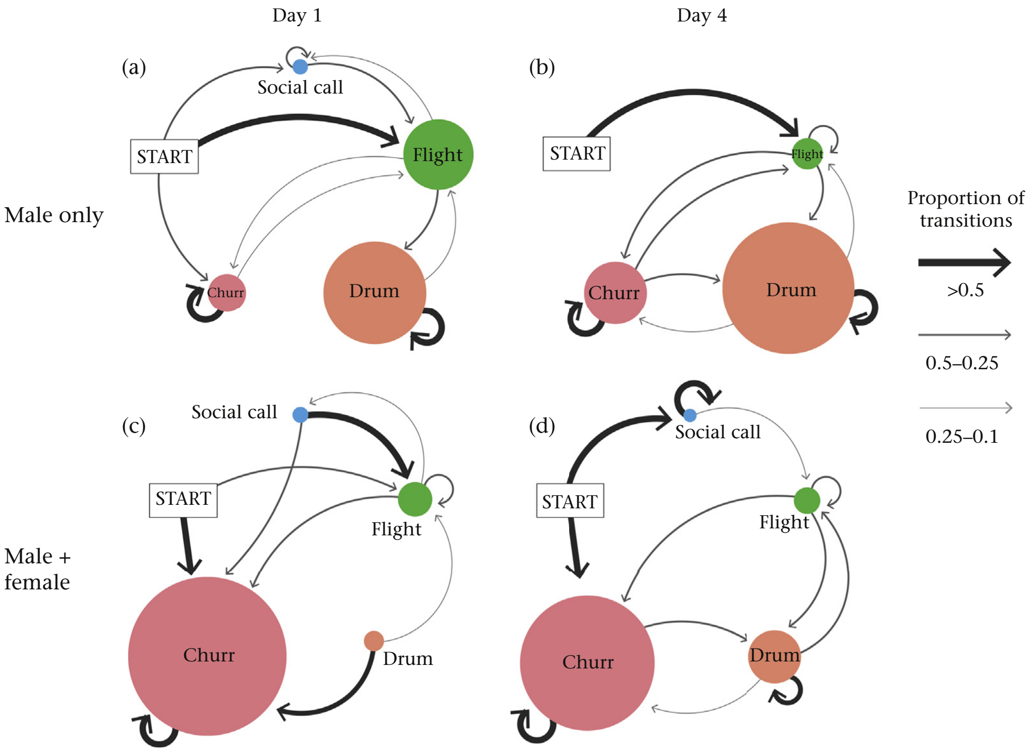

Figure 3. Transitions between key locomotion and signalling behaviours produced by male red-bellied woodpeckers during a 10 min simulated territorial intrusion: (a) on Day 1 (before any wins) in the absence of a female; (b) on Day 4 (three previous wins) with no female present; (c) on Day 1 with a female present; and (d) on Day 4 with a female present. Each circle is drawn to scale with number of behaviours produced, while arrow colour and width represent transition frequency. Only transitions with rates >0.1 are shown.

similarly to experimental males on Day 1 when presented with conspecific playback afterwards. Beyond the speed and intensity of territorial defence, we also found that the order in which males deployed different behaviours changed after repeated wins, an aspect of animal behaviour that is increasingly recognized as functionally significant (Suzuki, Wheatcroft, & Griesser, 2017). Specifically, males switched more frequently between different signals after forming a winner effect, a change that is associated with increased territorial aggression in other species (Horn & Falls, 1991; Kramer, Lemon, & Morris, 1985; Langmore, 1997).

At the same time, we also found that real-time shifts in social context, as marked by the arrival of a female conspecific, reshaped male behaviour both independently and in conjunction with the winner effect. First, males drummed less overall when a female observed trials staged both on the first and fourth days, but there was no overall change in male vocal behaviour. In terms of approach dynamics, a female's presence effectively reversed the winner effect, as males took longer to respond to playback after winning if a female was present. Both findings indicate that changes in social context effectively attenuated the winner effect, either dampening or eliminating how it reconfigured male behaviour. By contrast, the effect of female presence on male behavioural transition rates took place alongside the winner effect: males made more transitions to vocal behaviour both before and after experiencing multiple wins, while still transitioning more between different agonistic signals on the fourth day. Therefore, context sensitivity is a striking feature of the winner effect in this species, impacting how past experiences influence future behavioural strategies.

In addition to providing the first evidence showing how the winner effect reshapes how free-living animals manage territorial competition during the breeding season, our results also contextualize previous work showing that this mechanism is sensitive to an animal's physical and social environment (Fuxjager et al., 2009; Hirschenhauser et al., 2013). In both cases, the winner effect does not form in contexts where escalating aggressive behaviour would be unhelpful or even costly.

A Context-sensitive Winner Effect

An effective behavioural strategy should be sensitive to the different social context set by the presence of friendly individuals, such as the social mate (Ashbrook, Wanless, Harris, & Hamer, 2008). Indeed, we found that the winner effect's influence on male behaviour was attenuated during trials when a female was also present. Whether this attenuation reflects a change to the formation and/or development of the winner effect remains to be seen. Nevertheless, the social context defined by female attendance in territorial disputes appears to be one in which mounting a maximal agonistic response is no longer relevant and/or favourable.

One reason for this may be that female attendance to territorial competition decreases the necessity for a high-intensity response by males. Indeed, other woodpecker species specifically coordinate their territorial response when faced with more threatening intruders (Schuppe et al., 2016). However, this is unlikely to be the case for red-bellied woodpeckers, as females are not known to participate in conspecific territorial defence (Kilham, 1961) and acted as observers during all of our experimental trials. Instead, we suspect that male emphasis on vocal behaviour during trials with a female observer suggests that males are managing the competing social demands of communicating with both an antagonistic intruder and their social mate, because elevated aggression is no longer beneficial and/or is costly in this context. This may be the case since highly aggressive displays (such as drums, which were produced less in the presence of a female) could be threatening to both male and female conspecifics, and thus negatively impact the pair bond. This would be consistent with other studies showing that males attend to female reactions during display to avoid startling them with threatening behaviours (Patricelli et al., 2006).

Adaptive Value of the Winner Effect: the Pendulum Model

Our results provide empirical support for the hypothesis that the winner effect evolved because it allows animals to maximize the efficiency with which they resolve contests, while minimizing the costs of unnecessary competition (Fuxjager & Marler, 2010). Like many other phenotypes, territorial aggression exists on a continuum with steep costs incurred by individuals at either extreme. For example, the costs of exhibiting low or no aggression can be steep in terms of an individual's ability to maintain a high-quality territory and/or attract a mate (Pryke & Griffith, 2009; Webster, Ward, & Hart, 2009; West-Eberhard, 1983), especially if mate choice is partially mediated by competition (Stern & Servedio, 2017). At the other extreme, more investment in agonistic behaviour is associated with numerous costs in terms of elevated mortality (Marler & Moore, 1988), greater energetic demands (Matsumasa & Murai, 2005), trade-offs with parental care (Duckworth, 2006) and the risk of injury or ornament damage due to fighting (Gosling, Petrie, & Rainy, 1987). The winner effect may thus be a way to avoid the costs at either extreme by allowing an individual to reversibly increase its aggression according to the contextual demands. Therefore, we suspect that the winner effect is adaptive because it allows an individual to benefit from better territorial defence associated with rapidly escalating agonistic behaviour, while avoiding the costs this would otherwise incur.

By negotiating the costs and benefits of high- and low-aggression strategies, the winner effect may help maintain a behavioural optimum between these two extremes. In the absence of the winner effect, the evolutionary ‘solution’ to negotiating between high- and low-aggression strategies would probably be stabilizing selection around an optimum in the middle (McGlothlin, Jawor, & Ketterson, 2007; Singleton & Hay, 1982). However, this process favours a reduction in variation about the optimum. Considering that social behaviour phenotypes exhibit more standing variation than various other traits (Miles, Vitousek, et al., 2018), this makes it unlikely that agonistic social behaviour avoids unfavourable extremes by stabilizing selection alone.

Moreover, the prevalence of behavioural syndromes further makes it unlikely that a single behavioural ‘solution’ exists to manage territorial aggression. The complexity of social behaviour often gives rise to personality differences between individuals (MacKay & Haskell, 2015), which can specifically underlie performance during competition (Fuxjager, Montgomery, Becker, & Marler, 2010). Indeed, the sheer variation in male responses to playback suggests this is also likely to be the case for red-bellied woodpeckers. Still, our results suggest that the winner effect may be an alternative route by which behavioural optima are maintained, considering how male behaviour changed during the experiment despite natural variation in behaviour. Indeed, the winner effect is specifically thought to operate independently of individual variation in complex traits such as competitive ability (Hsu et al., 2006; Oyegbile & Marler, 2005). In this respect, the winner effect apparently offers a platform for aggressive behaviour to act like a pendulum, swinging between behavioural extremes in response to experience and social context. Our results are consistent with this model, where the winner effect pushes the behavioural pendulum towards elevated aggression and increases the effectiveness of territorial strategy (in the absence of a female observer). However, the arrival of a female triggers a swing in the opposite direction, at least in terms of behavioural output and approach latency.

Do all species stand to benefit from mechanisms such as the winner effect that allow for agonistic behaviour to be fine-tuned to different contexts? Although the winner effect has been studied in only a few species, the information we have suggests that different life history traits may increase or decrease the adaptive value of the winner effect. In particular, monogamous species with biparental care experience social as well as physiological costs for behaving aggressively in inappropriate contexts (Duckworth, 2006; Marler & Moore, 1988; O'Loghlen & Rothstein, 2010), which suggests that a robust winner effect should be more likely to emerge in these species. Indeed, well-studied California mice, *Peromyscus californicus*, are also monogamous, territorial and biparental (Gubernick & Alberts, 1987; Trainor & Marler, 2001), and they form a strong winner effect when fighting in familiar territory (Fuxjager & Marler, 2010; Fuxjager et al., 2009). In the same vein, the relative cost of losing a territory (or conversely, the benefit of retaining one) should also impact the adaptive value of the winner effect. The steep consequences of territory loss therefore suggest the winner effect is adaptive, as it provides a platform for individuals to rapidly increase their aggressive response once a potential usurper arrives in the area for breeding (Fuxjager & Marler, 2010; Fuxjager et al., 2011). The costs of territory loss, plus the fact that a separate host of 'loser effects' specifically act on individuals that lose a fight (Hirschenhauser et al., 2013; Oliveira, Silva, & Canário, 2009), suggests that future work including a losing condition will better contextualize our understanding of winner/loser effects in the natural world.

This same model may point to the functional significance of the mechanisms encapsulated by the 'challenge hypothesis', wherein seasonal fluctuations in circulating testosterone allow individuals to respond more aggressively to territorial intrusion without elevating an individual's standing aggression overall (Wingfield, 1994; Wingfield, Hegner, Dufty, & Ball, 1990). Although the relationship between testosterone release and territoriality is often discussed through the lens of these season-wide timescales, short-term increases in circulating testosterone are also associated with shifts in social context (Gleason, Fuxjager, Oyegbile, & Marler, 2009; Goymann, 2009; Hirschenhauser et al., 2013) and even underlie the winner effect itself (Apfelbeck et al., 2011; Fuxjager et al., 2009; Oyegbile & Marler, 2005). Indeed, not only is the winner effect's formation associated with elevated testosterone release, but administering testosterone can induce the winner effect in species that would not form one naturally (Fuxjager et al., 2011). The relationship between seasonal neuroendocrine changes and the winner effect remain unknown, but future studies integrating these two perspectives should prove fruitful.

Conclusions

In this first study to directly test whether the winner effect influences behaviour in a free-living population, we have shown that winning repeated territorial contests prompts wild male woodpeckers to behave more aggressively in subsequent intrusions. This suggests that the winner effect, a widespread mechanism of behavioural flexibility, may have a potent influence on the evolution of territorial strategies in wild animals. We then found a new instance of context sensitivity in the winner effect: observed increases in aggression disappeared when a female woodpecker was also present during territorial intrusions. The winner effect may thus have broader importance as a mechanism that facilitates the maintenance of aggressive optima on day-to-day timescales within an individual's life span.

Author Contributions

M.C.M. and M.J.F. developed the study, analysed the data and drafted the manuscript. M.C.M. conducted fieldwork to collect the data.

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Appendix

Table A1
Fixed effects of trial daytime spent actively responding on male red-bellied woodpecker behavioural output during 10 min simulated territorial intrusions

Response	*F*	*df*	*P*
No. of drums	2.42	1,12	0.146
No. of 'churr' calls	0.410	1,11.7	0.534
Total no. of displays	0.100	1,10.7	0.758

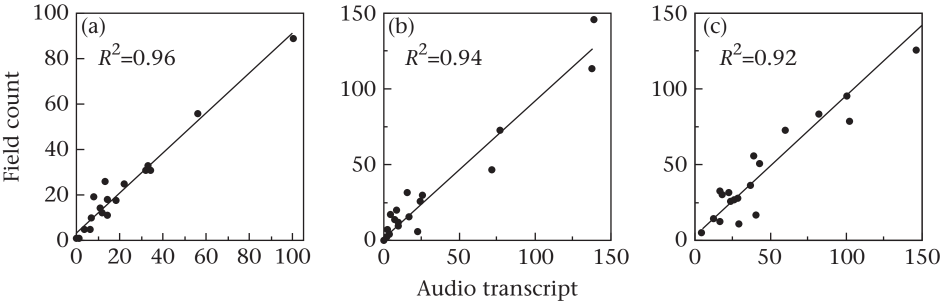

Figure A1. Relation between behavioural count data coded by two independent observers, first in the field and then from acoustic recordings on the computer. (a) Number of drums, (b) number of 'churr' calls and (c) the sum of both drums and 'churr' calls.