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Courtship display speed varies daily and with body size in the Ruffed Grouse (*Bonasa umbellus*).

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Abstract

Courtship displays are typically comprised of the same behavioral pattern, or patterns, repeated several times by males. Both the quantity and quality of the displays produced by a given male are not, however, constant. In some species, the number and/or quality of displays decreases over time, indicating fatigue. Conversely, other species engage in a warm-up period whereby the quality of the display improves after practice. Here, we test whether the drumming display of male ruffed grouse (*Bonasa umbellus*) changes in relation to the number of displays executed. Using a large number of recordings, our linear mixed models yielded a significant effect of cumulative number of drumming displays on the number of wingbeats per second, referred to as pulse rate. Across males, pulse rate is slowest when males begin drumming each day and increases until approximately 50 drumming displays have been produced. The rate of increase is also modulated by the night time low temperature such that cooler conditions are associated with lower pulse rates and the pulse rate increases at a slower rate, relative to the cumulative number of displays. The maximum pulse rate recorded and average pulse rate after 50 displays have been produced are inversely correlated with body mass such that larger males are slower than smaller males. The daily changes in pulse rate likely reflect both a warm-up period in the early morning hours and fatigue later in the day after more than 100 displays have been produced. Whether these dynamic changes in the production of a motor display are informative to females is unknown. However, we propose that daily changes in the production of motor displays may be a common feature of avian courtship that has gone relatively unnoticed, despite the potential for motor performance to be a trait that is important for female mate choice.

Introduction

Courtship displays are critical for reproduction in many animal species; individual differences in courtship behavior often form the basis of mate selection and as such, males with inferior performance fail to reproduce. Variation in courtship behavior within and among males can be manifested in different ways, depending on the type of courtship display being used. For instance, males can vary in how often a display can be repeated over time, or in the complexity of the individual components (Byers, 2010). Because courtship displays are performed repeatedly, the frequency and/or consistency of the performance can reflect a male's vigor. Females may then assess the performance capacity of a male as an indicator of quality (Ballentine, 2004; Byers, 2010; Sullivan & Kwiatkowski, 2007; Vannoni, 2009).

Performance of courtship displays not only vary among males within a population, it can also vary within males. Prolonged bouts of courtship displays can be energetically costly, leading to fatigue (Green, 1991; Mitchell, Poland, & Fine, 2008; Mowles & Jepson, 2015). For example, some males decrease how frequently they produce a display and/or the number of repetitions within a bout over time (Green, 1991; Lambrechts & Dhondt, 1988; Thorson, 2002). Frequent repetition of a display can also lead to structural changes in the signal, another potential indicator of fatigue (Vannoni, 2009). Fatigue does not, however, apply to all courtship displays. In side-blotched lizards (*Uta stansburiana*), push-up displays appear to be robust to the effects of fatigue (Brandt & Allen, 2004). Other studies even demonstrate a 'warm-up period' whereby the courtship signal increases in intensity and/or frequency after a number of displays have been performed. For example, male túngara frogs (*Engystomops pustulosus*) begin calling at slower rates, with shorter durations, and lower amplitudes (Pauly, 2006). As their vocal sac inflates, they increase call rate, duration, and amplitude with consecutive calling bouts, which increases

their attractiveness to females (Pauly, 2006). Both fundamental frequency and amplitude of zebra finch (*Taeniopygia guttata*) song also increase throughout the morning, to a maximum during the afternoon and then decrease in the evening (Wood, 2013). Perhaps the strongest evidence for a warm-up period is a recent study on Adelaide's warblers (*Setophaga adelaidae*). Male warblers improve their song performance throughout the morning and the amount of improvement is dependent on the cumulative number of songs sung (Schraft, 2017). That is, the more male warblers sing, the better their performance during the morning hours. Thus, species can vary in how consistently a courtship display can be produced and can even vary in whether performance declines or improves over time.

In birds, the majority of research into inter- and intra-individual variation in courtship displays has focused on vocalizations. Avian courtship can, however, include a wide range of complex motor acts that are also subject to variation across and within individuals. Despite the widespread occurrence of sonations, dances and various plumage displays, there are only a handful of studies addressing inter- or intra-male variation of motor displays in birds (J. Barske, Fusani, L., Wikelski, M., Feng, N.Y., Santos, M., Schlinger, B.A., 2014; J. Barske, Schlinger, Wikelski, & Fusani, 2011; Fusani, Giordano, Day, & Schlinger, 2007; L. T. Manica, Graves, Podos, & Macedo, 2016; L. T. Manica, Macedo, R.H., Graves, J.A., Podos, J., 2017; Ota, Gahr, & Soma, 2015). Motor displays that involve fine and/or intense motor control are likely to vary both within and among males because their dependence on muscle performance makes them susceptible to fatigue and potential candidates for warm-up periods. However, whether the performance of these kinds of motor displays changes across successive bouts within a day is unknown in birds. One of the difficulties in measuring variation of motor displays in birds is quantification (Byers, 2010). By definition, motor displays involve movement and males of

most species rarely remain in one spot when they are performing displays, which can make it difficult to measure variation within and among males. A rare exception to this is the ruffed grouse (*Bonasa umbellus*), a gamebird species endemic to North America. During the breeding season, male ruffed grouse perform a display known as drumming, which consists of a male beating its wings while standing on a log, tree root or other object on the forest floor (Hjorth, 1970) (Figure 1). The wingbeats create a low frequency drumming sound (Garcia, Charrier, Rendall, & Iwaniuk, 2012; Hjorth, 1970) that can be heard up to 1000m away. Unlike other species that perform complex motor displays, ruffed grouse remain standing in one spot during their display and return to the same display site daily. The consistent use of a drumming structure (e.g., log, tree root or rock) throughout the breeding season (Berkeley, 2014) permits repeated measurements of individuals over time in ways that are not readily feasible in other species.

Despite being a relatively common species with a wide distribution (Rusch, 2000) there are relatively few behavioral studies of ruffed grouse and earlier studies on drumming behavior relied heavily on small samples sizes or anecdotal observations (Archibald, 1976; Aubin, 1972). More recently, we analyzed the acoustic structure of drumming displays across over 20 males and concluded that they differ significantly in pulse rate, which refers to the number of wingbeats per second within a display (Garcia et al., 2012). However, we were unable to answer two key questions in this initial study. First, is pulse rate stable throughout the day? Males can produce more than 300 drumming displays per day (O'Neil, 2016). This relatively large number of displays could cause fatigue over time, which, in turn, could be reflected in a decrease in pulse rate over consecutive displays. Alternatively, male grouse might be able to drum consistently at the same pulse rate or even increase in pulse rate with increasing numbers of displays (i.e.,

warm-up period). Second, does pulse rate reflect body size or morphology? Many avian courtship displays reflect some component of body size or condition (J. Barske et al., 2011; Juola, 2011; Marks, 2010; Podos, 2001) and it is possible that variation among males (Garcia et al., 2012) arises from individual differences in body size. Here, we aimed to answer these two questions through the analyses of recordings made of actively drumming males across several years and comparisons with morphometric measurements.

Materials and Methods

Field sites and data collection

Male ruffed grouse were studied at two field sites. The first site is near Buck Lake, Alberta, Canada (52.97° N, 114.77° W) where we recorded males during April and May from 2013-2015. The site is a mixed boreal forest comprised primarily of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) stands mixed with assorted conifer species, shrubs and small muskeg patches. The second site was southwest of Beaver Mines, Alberta, Canada (49.47°N, 114.22°W). This site is along the eastern slope of the Rocky Mountains, but the lower elevations contains a comparable forest type to Buck Lake with trembling aspen and white birch (*Betula papyrifera*) stands mixed with assorted conifer species, shrubs and a few small muskeg patches. We used this second site in 2016 to sample individuals for a population genetics study (Jensen, 2019).

Males were located by ear during morning hours (04:00-11:00) and their drumming logs were marked with handheld GPS units (GPSMAP 64s, Garmin, Olathe, KS, USA). SongMeters (SM2 and SM2+ models, Wildlife Acoustics Inc, Maynard, MA, USA) were placed within 10 meters of their primary drumming log for 3-35 days to record the focal male's drumming

behavior remotely. Each male was recorded continuously from 00:00-23:30. The 30 minute interval reduced how often the batteries had to be changed, especially early in the season when the recorded low temperatures are generally $\leq -5^{\circ}\text{C}$. The sampling rate was set at 44.1 kHz and all files were saved as uncompressed WAV files.

Some males have secondary logs that they may switch to during the breeding season, but these other logs are usually located within close proximity of their primary log (Gullion, 1967, 1984) and in most cases, males could still be heard in the recordings at these secondary (and even tertiary) logs. Males were not individually marked, but they maintain the same drumming log(s) during a breeding season (Berkeley, 2014) and the identity of each male could be checked by examining their individual pulse rate and pulse number (Garcia et al., 2012).

In 2016, we recorded 25 males for 2-3 days with SongMeters prior to trapping. All grouse were trapped within 4 days of completing the recordings, to ensure that males did not abandon their logs and that the recorded pulse rate reflected current body mass and condition. Males were caught using mirror traps (Gullion, 1965) or a lift net (Fischer, 1974). Mirror traps were secured to males' drumming logs adjacent to the drumming stage. The lift net was set on the drumming log the day before trapping and then triggered manually by an observer the following morning when the male was standing on top of the net (Fischer, 1974). Once caught, each male was placed into a dark-coloured pillowcase, weighed with a spring scale ($\pm 5\text{g}$) and linear measurements taken of the tarsus with plastic calipers ($\pm 0.5\text{ mm}$) and the wing chord with a wing rule ($\pm 1\text{mm}$). Finally, blood samples were taken using brachial venipuncture for a population genetics study (Jensen et al., 2019), after which the grouse was released. All procedures adhered to the Canada Council for Animal Care regulations, were approved by the

University of Lethbridge Animal Welfare Committee and collected under research permits issued by Alberta Environment and Parks.

Acoustic Analyses

Pulse rates of the drumming displays were measured using the pulse train analysis tool in Avisoft SASLab Pro (v5.1, Avisoft Bioacoustics, Berlin, Germany). For all pulse train analyses, the initial four pulses (quartet) were excluded to ensure consistency across recordings. The quartet is a series of four low amplitude wing beats at the beginning of each drumming display (Figure 2). This portion of the display is often masked by background noise and therefore was excluded to increase the sample size of analyzed displays across and within individuals. Only drumming displays with high quality recordings in which every individual pulse could be distinguished from background noise were included in the pulse train analyses. We focused our analyses on overall pulse rate (Garcia et al. 2012), the number of wingbeats per second, because the speed of the display is more likely to be subject to fatigue or warming up than the number of pulses produced.

To test for variability in pulse rate, we first analyzed 6 drumming displays per hour over 24 hours for three males recorded for two ($n = 1$) or three ($n = 2$) days each (23-26 April 2015). This amounted to an analysis of 755 drumming displays across the three males. For our remaining analyses, we focused on measuring drumming displays from 00:00-10:00. This time frame was selected because all males drummed in the morning hours of every recording day, but afternoon and evening drumming activity was highly variable both across and within individuals. Recording quality was sufficient to analyze 37 individuals in total, for which we analyzed 6 drumming displays per sampling hour over a period of 5-28 days for a total sample of 5,123

displays. For each male, we also recorded how many times they drummed each day and the number of each drumming display that we analyzed for pulse rate. This enabled us to test whether pulse rate changed as a function of the number of drumming displays executed (Schraft et al. 2017) and we refer to this variable as cumulative drumming count.

Statistical Analyses

Pulse rate between 00:00-10:00

We used Linear Mixed Models (LMM) fitted with Maximum Likelihood, to investigate how pulse rate varied as function of cumulative drumming count, midnight temperature, day in the season and year. All continuous predictors were scaled and centered before inclusion in the models, except year, which was treated as a categorical predictor (4 levels: 2013, 2014, 2015 and 2016). If changes in pulse rate reflect ‘warm-up’ and/or fatigue effects, then pulse rate should be non-linearly related to the cumulative drumming count. Thus, we modelled the relation between pulse rate and cumulative drumming as either a linear or a quadratic equation. In all cases, we included an interaction between cumulative drumming and midnight temperature as temperature could influence drumming activity. Temperature data was obtained from Environment and Climate Change Canada historical data (http://climate.weather.gc.ca/index_e.html) recorded at weather stations in Rocky Mountain House (52°25'17.006" N, 114°54'44.003" W) or Beaver Mines (49°28'04.500" N, 114°10'30.000" W), the closest two weather stations to our field sites. All three models also included year as a fixed effect and the Julian calendar date as a covariate and random slopes and intercepts for individual grouses. In addition, we constructed two ‘null’ models. The first null model (Null model 1) only included an intercept and random effects while the second null model (Null model 2), was more ‘informed’ and as such included random effects

and all fixed effects and covariates, except cumulative drumming count, on the basis that pulse rate variation may be explained by changes in temperature, year or day in the season, irrespective of cumulative drumming.

To compare models and determine which combination of parameters best explained variation in pulse rate, we used the multi-model inference approach, which compares models using a weighted ranking technique (e.g., AIC), to quantify the relative support for each of the models. For inference, we used model weights, which represent normalized ratios of the difference of AIC between the target model and the best model in the candidate set. These model weights can be interpreted as probabilities that a given model is the best model in our set of models (Anderson, 2007). We visually inspected diagnostic plots to check model assumptions, computed marginal and conditional pseudo- R^2 values (Nakagawa, Johnson, & Schielzeth, 2017) to assess model goodness of fit and used cross-validation procedures to assess model over-fitting tendency based on the comparison of RMS values (mean + standard deviation (SD)) between training and cross-validated datasets. For the cross-validation, we used two procedures to separate the dataset into the training and test set to assess the impact of the random effects on model predictions. In the first procedure we used data from all but one bird to train the model and predicted data for the remaining bird, repeating this process 37 times, until all birds had been used as the test set. The second procedure performed the k-fold cross-validation approach, using $k=37$. We calculated mean and SD RMS for both training and test sets and for both procedures.

Exhaustive sampling

We used the same approach as for the larger dataset, the only difference being the variables included in the models. We included cumulative drumming count and grouse identity

as fixed effects, but not date or midnight temperature as not all males were sampled on the same day (and thus the date/temperature variables were collinear with grouse identity). Grouse identity was included as a fixed factor rather than a random effect because of the low number of levels (3 individuals), which renders estimates of random terms unreliable. As no random effect was included, we implemented linear models (LMs), used R^2 values to assess model goodness of fit and assessed model over-fitting tendency using a 10-fold cross-validation procedure.

Pulse rate and body mass

To test for an association between pulse rate and our morphometric measurements, we used least-squares linear regressions. Our pulse rate measurements included the absolute minimum and maximum pulse rates, and the difference between them, recorded between 00:00 and 10:00 across at least two days for each male that we trapped. In addition, we calculated the average pulse rate after at least 50 drumming displays were performed (see below). These four pulse rate measurements were then compared against each of the morphometric measurements: wing chord, tarsus length, and body mass. We attempted to estimate body condition using residuals from a regression of body mass against tarsus length (Green, 2001; Schulte-Hostedde, Zinner, Millar, & Hickling, 2005) as well as a ratio of body mass:tarsus length (Schamber, Esler, & Flint, 2009). However, both the residuals and ratios were significantly correlated with body mass (p 's < 0.01 ; $R^2 = 0.74$ and 0.57 , respectively), indicating that both reflect body size and not condition. We therefore restrict our analyses to body size.

Results

Pulse rate between 00:00-10:00

In the analysis of pulse rate in the morning hours, the model that received the highest support was a quadratic relationship between pulse rate and cumulative drumming count (Table 1, Figure 3a). Results of cross validation tests using both the ‘leave one bird out’ and 37-fold cross-validation procedures yielded no evidence that the quadratic model was over-fitting the data (Table 2). Further, even though RMS values are somewhat higher when random effects are controlled, which is to be expected given the high inter-individual variation (see below), prediction errors remain overall low (Table 2), confirming that the model reliably approximates the observed pattern.

As shown by the standardized beta estimates (Table 3), cumulative drumming count has a large, positive effect on pulse rate (linear term $\text{Beta}=0.286$, $p<0.001$). Initially, pulse rate increases linearly with cumulative drumming, but then inflexes negatively, such that the rate of change becomes more gradual (quadratic term $\text{Beta}= -0.125$, $p<0.001$). Furthermore, this pattern is modulated by midnight temperature, such that the linear increase is steeper in cold conditions as opposed to milder temperatures (Cumulative drumming * midnight temperature interaction: $\text{Beta} = -0.028$, $p<0.001$), and the inflexion in the rate of increase in pulse rate is steeper at higher midnight temperatures (quadratic Cumulative drumming term * midnight temperature interaction: $\text{Beta} = 0.014$, $p=0.021$, Figure 3a). It is also worth noting the large random effect variance and high intra-class correlation, which indicate high inter-individual variation, but low within-individual variation (Figure 4). In other words, pulse rate is highly variable among individuals, but consistent within individuals.

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Exhaustive sampling

In the analysis of pulse rate throughout the day, the model that received the highest support was the model that fit a quadratic relationship between pulse rate and cumulative drumming count (Table 1), and cross-validation tests showed no evidence of over-fitting issues (Table 2). As for the full dataset of 37 males, the results indicate that there is an initial increase in pulse rate as cumulative drumming count increases ($F=314.68$, $p<0.001$), followed by a negative inflexion ($F=49.89$, $p<0.001$). This pattern is consistent across the three males, although there are significant differences in pulse rate among individuals ($F=1889.49$, $p<0.001$, Table 4, Figure 3b).

Pulse rate varies with body mass

No significant relationship was detected between minimum pulse rate and body mass ($F = 2.18$, $df = 1, 23$, $p = 0.15$, Figure 5a). However, both maximum pulse rate ($F = 7.44$, $df = 1, 23$, $p = 0.01$, $adj. R^2 = 0.21$, Figure 5b) and difference between maximum and minimum pulse rate ($F = 4.68$, $df = 1, 23$, $p = 0.04$, $adj. R^2 = 0.13$, Figure 5c) significantly decreased with increasing body mass. Based on the analyses above indicating an effect of cumulative drumming on pulse rate, we also calculated the average pulse rate after a minimum of 50 drumming displays as pulse rate of displays after this point have stabilized and are maintained throughout the rest of the morning hours across individuals (Figure 4). This average pulse rate also significantly decreased with increasing body mass ($F = 7.85$, $df = 1, 23$, $p = 0.01$, $adj. R^2 = 0.22$, Figure 5d). In contrast to our analyses of body mass, pulse rate did not vary significantly relative to tarsus length or wing chord length (all p 's ≥ 0.39).

Discussion

Based on our analyses, the pulse rate of ruffed grouse drumming displays changes based on the cumulative number of displays produced. That is, pulse rate increased as more and more drumming displays were produced up to a certain point and then begins to decline. The increase in pulse rate occurred across all males that we recorded and was modulated by overnight temperatures such that males drummed at slower pulse rates on cold nights compared with warm nights (Figure 3a). Further, pulse rate varied inversely with body size such that larger grouse were slower and had less of a difference between minimum and maximum pulse rate (Figure 5). These results provide novel insights into the drumming display of ruffed grouse, but also suggest that warm-up periods and fatigue are factors that can simultaneously affect non-vocal courtship display production in birds.

In an earlier study, Garcia et al. (2012) stated that pulse rate appeared to be relatively constant within displaying grouse, but this was based on relatively few recordings over 2-3 days. Although our data shows that pulse rate is dynamic throughout the day based on temperature and drumming activity, it also demonstrates relatively low variability within males compared to inter-individual variation. Our LMMs had large random effect variance and high intra-class coefficient, indicative of high variation among individuals, but low variation within individuals. This is also evident in examining pulse rate relative to number of drumming displays across all 37 males (Figure 4). Thus, even though all males increase their pulse rate relative to the number of drumming displays produced, they all do so within a relatively narrow range of pulse rates.

The increase in pulse rate with the cumulative number of drumming displays is indicative of a warming up effect. All males recorded began their drumming activity with lower pulse rates that progressively increased with the number of displays performed. Importantly, our model

inference approach shows that out of all the predictors investigated in this study, cumulative drumming was the single most important explanatory variable (quadratic models weights =1, Table 1). This appears to parallel patterns observed in vocalizing frogs and songbirds where amplitude and frequency increase over successive calling bouts (Pauly, 2006; Schraft, 2017; Wood, 2013). In human athletes, one of the purported benefits of warming up is an increase in muscle and core temperatures that ultimately improve performance through decreased resistance, faster metabolic reactions and increased nerve conduction rates (Bishop, 2003a, 2003b). When males first start drumming, it is typically after ≥ 4 hours of no drumming activity (O'Neil, 2016), even if a male first begins drumming just after midnight. A lower pulse rate after several hours of no drumming suggests that the muscles require activity in order to achieve higher pulse rates. In addition, midnight temperature modulated the change in pulse rate such that there is a steeper increase and the maximum pulse rate reached is lower on colder nights than warmer nights (Figure 3a). The low initial pulse rate following a period of no drumming activity coupled with a temperature dependent effect and an effect of cumulative displays on pulse rate all suggest that males are warming up daily.

Warm up is not, however, the only phenomenon affecting daily variation in pulse rate. In both the birds sampled only in the morning and those that were exhaustively sampled, the relationship between pulse rate and cumulative drumming displays is an arc (Figure 3). This arc shape indicates that pulse rate declines after 100+ drumming displays, suggesting that males are also experiencing fatigue. A similar curvilinear relationship, but even steeper, occurs in the amplitude and frequency of zebra finch song syllables (Wood, 2013). There are several potential mechanisms that could explain daily variation in song or the drumming display. Wood et al. (2013) suggested that in zebra finches this may be a byproduct of circadian rhythms in body

temperature and/or melatonin levels. The rising and falling phases in daily pulse rate variation could potentially reflect circadian physiology, but if that were the case, we would also expect drumming activity to be more consistent from one day to the next. Peak drumming activity typically occurs between 04:00 and 06:00, but males can start drumming anywhere from 00:00 to 05:00 and might drum throughout the entire day or stop at 10:00 and not drum until the following day (O'Neil, 2016). Some males drum consistently in the evening whereas other males never do. If drumming behaviour was primarily driven by endogenous factors, these patterns should be more consistent throughout our population. An alternative explanation for the curvilinear pattern in pulse rate is that the rising phase is due to warming up whereas the falling phase is due to fatigue. Without knowing the energetic costs of drumming or the effects of drumming activity on muscle temperature and physiology, this explanation is also speculative (Clark, 2012), but possible given that males can drum over 300 times per day (O'Neil, 2016) and the display appears to involve a significant amount of muscle mass.

Interestingly, pulse rate variation among individuals is correlated with body mass, but the correlation is negative. This negative correlation was present across three of the four pulse rate measurements and no significant correlations were detected when pulse rate was compared against tarsus or wing chord lengths. The amount of variation explained by the body mass-pulse rate relationships was not large (R^2 s = 0.13-0.22), but was consistent despite considerable variation across males (Figure 4). A negative relationship between wingbeat frequency and body size is often found in comparative studies (Altshuler, 2010; Darveau, 2005; Dudley, 1990) and is thought to be primarily a consequence of wing size. Although we observed no significant correlation between wing chord and pulse rate, it is possible that the body mass-pulse rate correlation reflects a similar, underlying physical constraint. What that physical constraint is

cannot be determined at this time, but detailed kinematic studies of the drumming display could provide some insights.

In a similar fashion to other bird species (Fuxjager, 2015; Hjorth, 1970; Johnsgard, 1994), the drumming display is only one part of ruffed grouse courtship. As a female approaches, the male ceases drumming and engages in a ruff and tail fanning display (Hjorth, 1970). This visual display likely forms the basis of ultimate mate selection, but whether females also choose which males to visit based on drumming behaviour is unknown. Females do range over large areas during the breeding season (Maxson, 1978; Whitaker, 2007) and at least one study found that females will visit the drumming sites of several males (Brander, 1967). The galliform auditory system is tuned to low frequencies (Corfield, 2013; Hill, Koay, Heffner, & Heffner, 2014) and highly sensitive to temporal differences (Agmon-Snir, 1998), so females could detect differences in pulse rate across or within males. However, until female mate choice experiments and/or more detailed study of female movements are conducted, whether the variation we documented is relevant to mate choice remains unknown.

Drumming is a relatively simple motor display: it is a single repeated element. In contrast, other bird species incorporate a diverse range of movements into their displays (Fusani et al., 2007; Fuxjager, 2015; Hjorth, 1970; Johnsgard, 1994; L. T. Manica et al., 2016; L. T. Manica, Macedo, R.H., Graves, J.A., Podos, J., 2017; Ribeiro, 2019). Each one of the elements used in these complex courtship displays might also vary throughout the day and with each performance, but studies comparable to ours have yet to be conducted in other species. Based on our results, we suspect that a warm-up period might be a common element in complex motor displays because of the potential benefits of increasing temperature on muscle performance (Bishop, 2003a, 2003b). Similarly, there may also be a decline in performance after a certain number of

displays have been completed, especially for displays that are energetically costly. Investigating daily changes in display elements is needed to better understand how recent activity or practice affects courtship performance, the effects of long display bouts and the physiological constraints underlying non-vocal courtship displays in general.

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Figure Legends

- Figure. 1** A three panel sequence of a male ruffed grouse (*Bonasa umbellus*) performing a drumming display while standing on a tree root.
- Figure. 2** A waveform of a drumming display recording with the initial four wingbeats, referred to as the quartet, indicated by the horizontal line.
- Figure 3** **a.** Pulse rate plotted against the cumulative drumming count, for all males sampled between 00:00 – 10:00. Each data point is a drumming display ($n = 5,123$) that was analyzed for an individual male (37 males in total). The solid lines show the fixed effect of cumulative drumming count for three levels of midnight temperature (low $< 1SD$, med= mean $\pm 1SD$, high $> 1SD$). The shaded areas indicate the 95% confidence intervals. **b.** Pulse rate plotted against the cumulative drumming count, for the three males sampled exhaustively throughout the day. Each data point is a drumming effect of cumulative drumming count for each of the three males.

- Fig. 4** Pulse rate plotted against the cumulative drumming count for all 37 males sampled. Each data point is an individual drumming display, with the blue lines indicating the fixed effect of cumulative drumming count modelled as a second-order polynomial and the shaded areas indicating the 95% confidence intervals. Each male's identity code is provided at the top of each scatterplot
- Fig. 5** Scatterplots of minimum pulse rate (**a**), maximum pulse rate (**b**), difference between maximum and minimum pulse rate (**c**) and the average pulse rate measured after 50 cumulative displays (**d**) plotted against body mass for 25 male grouse. In each plot, the solid line indicates the least-squares linear regression line and the dotted line is the 95% confidence interval. Only minimum pulse rate yielded a non-significant relationship.



Figure 1.

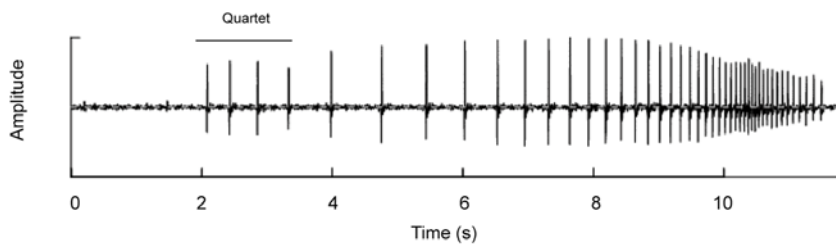


Figure 2.

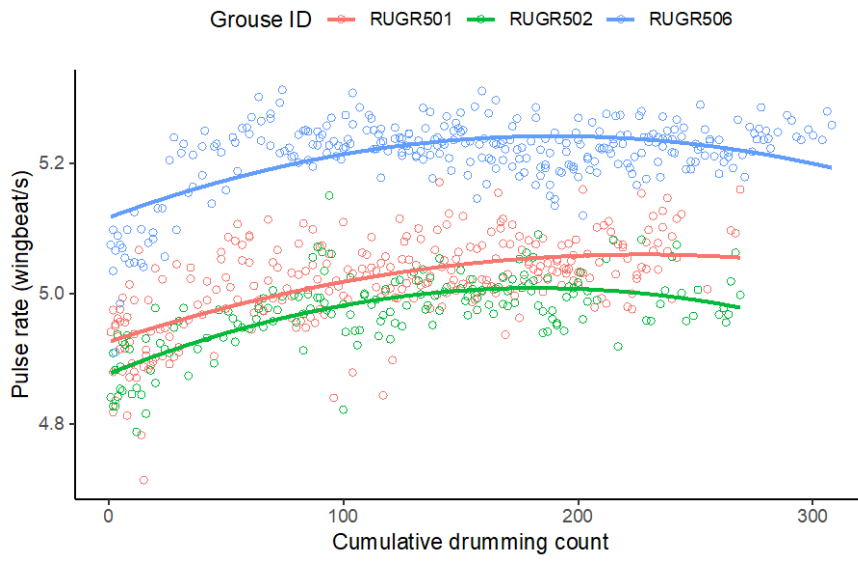
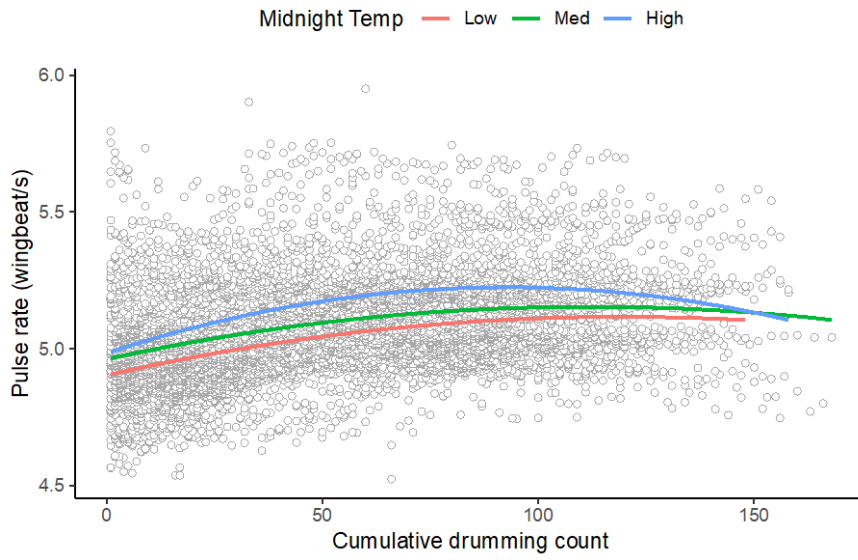


Figure 3.

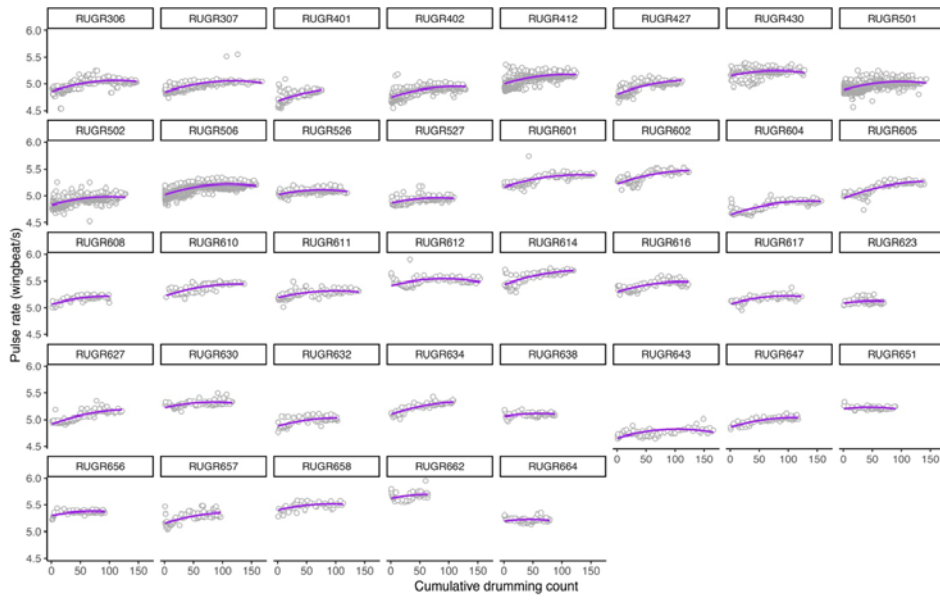


Figure 4.

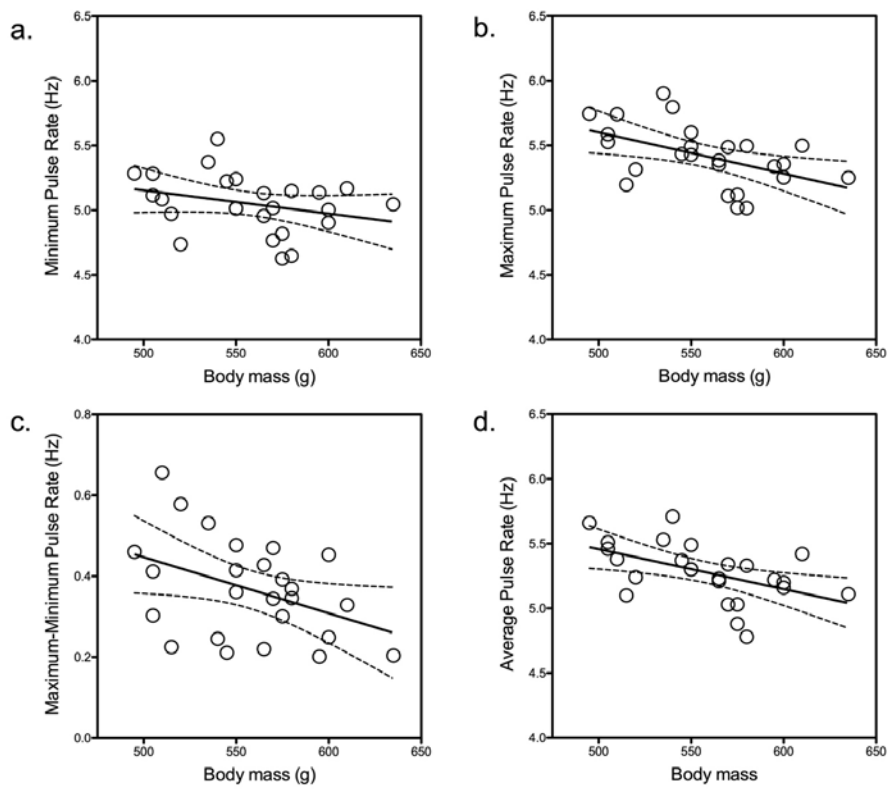


Figure 5.