



## Original Article

# Why does the rate of signal production in ectotherms vary with temperature?

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Received 23 February 2017; revised 14 May 2017; editorial decision 3 June 2017; accepted 26 June 2017; Advance Access publication 5 July 2017.

The rate of signal production by social ectotherms is often temperature dependent. This has been typically attributed to an underlying thermal constraint on physiology, but there are other reasons why signal rates might be correlated to temperature. We tested 3 hypotheses. The maximal performance hypothesis: temperature limits motor activity at cold and hot temperatures, which predicts a hump-shape function between signal rate and temperature. The metabolic rate hypothesis: the available energy released by metabolism increases exponentially with temperature, which predicts an exponential increase in signal rates with temperature. The recipient availability hypothesis: the number of potential receivers varies with temperature, and signalers change their signal rates accordingly, which predicts an indirect association between signal rate and temperature. We tested these hypotheses using field data on the rate of advertisement display production by territorial Jamaican and Puerto Rican *Anolis* lizards from a variety of thermal environments, coupled with extensive observations on one montane population of *A. gundlachi*. In both cases, the slopes of display rate as a function of ambient temperature were statistically indistinguishable from slopes predicted by the performance hypothesis. Support for the other 2 hypotheses was weak or equivocal. This is the first study to test alternative hypotheses of why signal rates and temperature in ectotherms are correlated and to indicate that thermal performance curves measured in the lab can reliably predict important social behavior in the field.

**Key words:** animal communication, contextual reaction norm, plasticity, thermal environment.

## INTRODUCTION

Numerous studies on ectotherms have demonstrated that the rate of production and the structure of communication signals can vary as a function of ambient temperature. Examples come from a wide range of taxa, including insects (Walker 1975; de Vrijer 1984; Pires and Hoy 1992; Ciceran et al. 1994; Martin et al. 2000; Ritchie et al. 2001; Hedrick et al. 2002; Greenfield and Medlock 2007; Navia et al. 2015), anurans (Gerhardt 1978; Gayou 1984; Llusia et al. 2013), and fish (Connaughton et al. 2000; Papes and Ladich 2011; Ladich and Schleinzer 2015; Vicente et al. 2015). The phenomenon crosses sensory modalities and occurs for acoustic (e.g., Gayou 1984; Martin et al. 2000; and other references above), visual (flashing fireflies: Carlson et al. 1976; Michaelidis et al. 2006), olfactory (pheromone emission in moths: Liu and Haynes 1994; Webster and Yin 1997), and electric forms of communication (signal discharges in electric fish: Dunlap et al. 2000). Reptiles have been less

studied, but the distress calls of hatchling crocodiles (Garrick LD and Garrick RA 1978), the warning rattle of rattlesnakes (Rowe and Owings 1996), and the aggressive head-bob movements of lizards (Phillips 1995) have been shown to vary with air temperature.

The effect of temperature on ectotherm communication is often attributed to thermal constraints on physiology (e.g., Dunlap et al. 2000; Greenfield and Medlock 2007; Llusia et al. 2013; Ladich and Schleinzer 2015). Ambient temperature can have a direct impact on motor activities through the thermal dependence of physiological and biochemical factors involved in muscle function (Bennett 1980, 1984). For example, laboratory studies on lizards routinely document a hump-shape maximal performance curve in which locomotor performance (typically measured as maximal running speed) progressively increases with body temperature until peak performance is reached at moderately high temperatures, after which it decreases rapidly with temperature until locomotion ceases entirely (Lee and Badham 1963; van Berkum 1986; Angilletta et al. 2002; Lailvaux and Irschick 2007; Gunderson and Leal 2012; Kolbe et al. 2013; Logan et al. 2015). These maximal performance curves mirror the temperature-dependent curves for enzyme

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activity and other factors associated with muscle contraction (e.g., Bennett 1980, 1984), implying a causal link between behavior and underlying temperature-dependent physiology (Moberly 1968; Angilletta et al. 2002).

Based on this literature, Gunderson and Leal (2015) recently presented a *performance model* that predicts the relationship between activity rates and temperature for members of a given taxon. This model assumes that the physiological constraints that limit maximal performance (e.g., maximal running speed) also limit the rates of production of other types of behavior that depend on neuromuscular processes. Therefore, at any given temperature, animals engaging in physiologically demanding types of behavior (e.g., courting, fighting, signal production) will do so at rates proportional to their maximal performance capacity at that temperature. Given that the maximal performance curves of ectotherms are concave, the performance hypothesis predicts that the rate of signal production will exhibit a similar concave relationship with temperature. More specifically, it predicts that the upward and downward slope of the relationship between signal production and temperature for a given taxon will be comparable to the upward and downward slopes of the maximal performance curve for that taxon, and that signal rates will peak at a temperature that corresponds to the temperature at which maximal performance is highest.

However, there are other physiological explanations for why signal rates might change as a function of temperature. One such hypothesis is that signal rates vary with temperature because metabolic rates vary with temperature (Gillooly and Ophir 2010; Ophir et al. 2010). This hypothesis is based on the fact that metabolic rate increases as a function of body temperature (Gillooly et al. 2001), and this in turn dictates the amount of energy that is available to support physical activity. The *metabolic model* assumes that animals devote a fixed proportion of their available energy to signal production (Gillooly and Ophir 2010; Ophir et al. 2010), and that signal rates vary with temperature because metabolic rates are temperature dependent (Gillooly et al. 2001).

The metabolic hypothesis also generates quantitative predictions about how signal rates should change with temperature. In particular, it predicts that signal rate will monotonically increase as a function of temperature, and that for a given taxon, the slope of the relationship between signal rate and temperature will be the same as the slope of the relationship between mass-specific resting metabolic rate (RMR) and temperature for that taxon (Gillooly and Ophir 2010). This prediction is based on the underlying assumption that at any temperature, animals use the same proportion of their available energy for signaling, so that the slope of resting rate on temperature is comparable to the slope of the signaling metabolic rate on temperature (see Ophir et al. 2010). This hypothesis was originally tested using data on among-species variation in various aspects of acoustic communication in ectotherms and endotherms (Gillooly and Ophir 2010). More recently, it has been used to study intrapopulation variation in signal production as a function of temperature in a population of treefrogs (Ziegler et al. 2016; see Discussion).

Both the performance and metabolic models implicitly assume that the number of potential recipients for a given signal is largely irrelevant to signal rate. They both assume that signalers produce the maximum number of signals possible—contingent on performance or metabolic constraints—regardless of the number of potential receivers available to detect those signals. However, this assumption may not be valid for advertisement signals, which are not directed at specific individuals, but are instead broadcast to

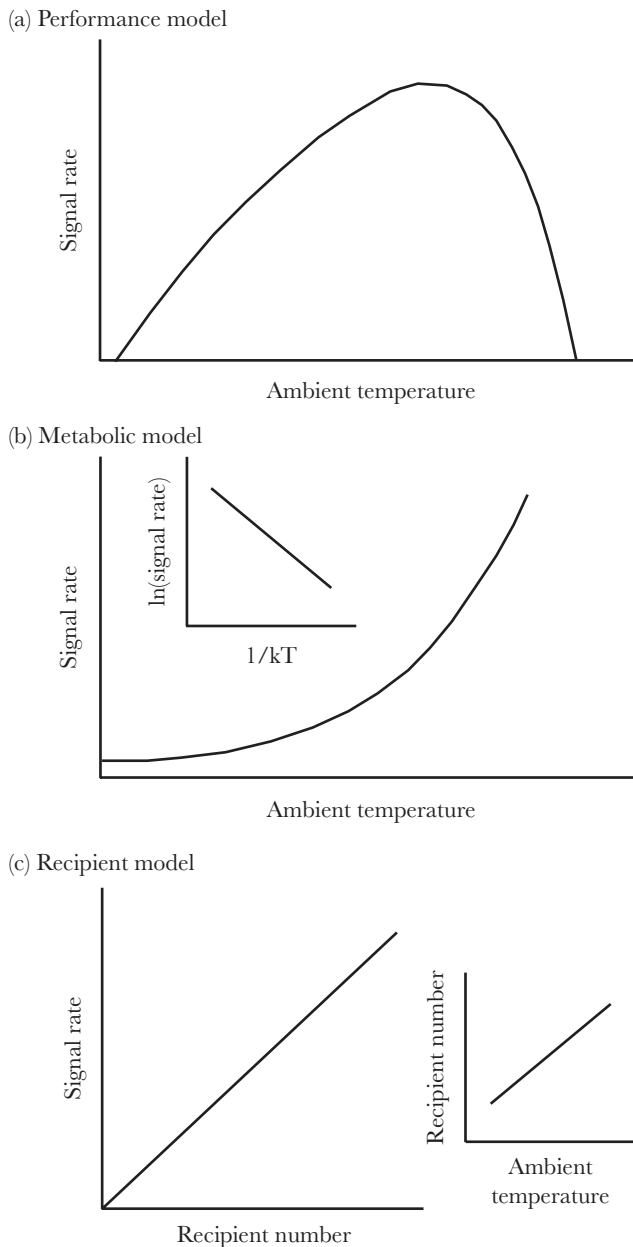
any and all of the potential receivers who might be able to detect them. If the net benefits of producing advertisement signals increase with the number of recipients receiving those signals, and if signals are costly to produce in terms of increased conspicuousness to predators (Simon 2007; Steinberg et al. 2014) and energetic expenditure (Leal 1999; Brandt 2003; Perry et al. 2004), then adjusting the rate of display production to the number of receivers should be adaptive. This idea is supported by field and laboratory studies that have demonstrated positive relationships between the production of advertisement signals and local population size or the number of potential recipients when an individual produces its signals (birds: Wellendorf et al. 2004; Sexton et al. 2007; Warren et al. 2013; fiddler crabs: How et al. 2008; insects: Aiken 1982).

The *recipient model* argues that the association between advertisement signal rates and temperature reported in field studies of ectotherms occurs because 1) the number of potential recipients for advertisement signals varies as a function of ambient temperature and 2) individuals monitor the number of recipients and increase the rate of production of advertisement signals when more recipients are present. With respect to the first assumption, there is considerable empirical evidence for ectotherms that the number of animals that are “active” (e.g., not in refuges or shelter sites) predictably varies as a function of temperature (insects: Corbet et al. 1993; Riis and Nachman 2006; Andrew et al. 2013; fish: Ord and Hsieh 2011; anurans: Cohen and Alford 1996; van Sluys and Guido-Castro 2011; snakes: Sun et al. 2001; Sperry et al. 2013; lizards: Huey and Webster 1976; Hertz and Huey 1981; Hertz 1992; Gunderson and Leal 2016).

These models can be distinguished empirically from one another in the following ways:

- *Performance model* (Gunderson and Leal 2015; Figure 1a): the curve for the relationship between signal rate and ambient temperature will have a similar shape as the curve for maximal performance versus temperature. Given the typical hump-shaped relationship between performance and temperature, this should result in an increase in signal rates over lower temperature ranges and a reduction in signal rates over higher temperature ranges. It also predicts that maximum signal rates should occur at the same temperature as peak performance.
- *Metabolic model* (Gillooly and Ophir 2010; Figure 1b): given that RMR increases exponentially with temperature (Gillooly et al. 2001), this hypothesis predicts an increase in signal rate as temperature increases, with no declines in signal rate at high temperatures. More specifically, the slope of the natural-log of signal rate on the inverse of ambient temperature will be the same as the slope computed for RMRs (Figure 1b, inset; see Materials and Methods).
- *Recipient model* (this study; Figure 1c): the number of potential recipients is related to ambient temperature, and signal rate is related to the number of potential recipients. The result is an indirect relationship between ambient temperature and signal rate because both of these variables are related to the number of recipients present in the surrounding environment.

These 3 hypotheses need not be mutually exclusive; for example, metabolic constraints might contribute to performance and to variation in recipient activity. We tested each hypothesis using field data on ambient temperature, territorial displays, and other variables in Jamaican and Puerto Rican *Anolis* lizards.



**Figure 1**

The rate of signals produced by ectotherms is expected to vary with ambient temperature because of direct temperature-dependent performance or metabolic constraints on signalers (a, b) or because of indirect temperature-dependent variation in receiver availability (c).

## The study system

Reproduction in Caribbean *Anolis* lizards is centered on adult males establishing exclusive territories to increase access to resident females (Jenssen et al. 1995, 2001). To advertise ownership and the continued occupancy of these territories to neighboring rivals, male lizards perform bouts of visual display from arboreal perches (Jenssen 1977; Ord 2008; Jenssen et al. 2012). These advertisement displays consist of an elaborate sequence of head-bob/push-up movements and the repeated extension of a large, colorful throat fan or dewlap. Males typically produce more than a hundred bouts of these displays over the course of a single day (Ord TJ, unpublished data). These displays are costly to produce, both in terms

of increased conspicuousness to predators (Simon 2007; Steinberg et al. 2014) and energetic expenditure (Leal 1999; Brandt 2003; Perry et al. 2004). Previous field studies indicate that the number of recipients of these displays probably varies with temperature, since the number of *Anolis* lizards active in the environment is often highest at warm temperatures, with fewer lizards in locations where they can be detected by human observers at either cool or hot temperatures (Huey and Webster 1976; Hertz and Huey 1981; Hertz 1992; Gunderson and Leal 2016).

In our first set of analyses, we used field data on the display rates of 16 Jamaican and Puerto Rican *Anolis* taxa living in different thermal environments to test the performance and the metabolic models at the genus level. We took advantage of published data on the thermal performance curves of anoles (Lailvaux and Irschick 2007; Logan et al. 2015, 2016; Gunderson and Leal 2016), and of the relationships between metabolic rates and temperature in anoles (Jenssen et al. 1996; Rogowitz 1996; Orrell et al. 2004; Steffen and Appel 2012; Kolbe et al. 2013), to estimate the relationships between display rate and temperature predicted by the performance and metabolic models for the members of this genus. Our goal here was not to predict the relationship between display rates and temperature for individuals in particular populations or species, but instead to determine which of these 2 models did a better job of accounting for the observed relationships between display rate and temperature observed for *Anolis* lizards from a wide range of thermal environments.

In a second set of analyses, we tested all 3 models (the performance, metabolic, and recipient models) using data for a single population of *Anolis gundlachi* living in the deep-shade forests of the Luquillo Mountains on Puerto Rico. Published data on the thermal performance curves and the relationship between metabolic rate and temperature were already available for members of this species at this locality (Gunderson and Leal [2016] and Rogowitz [1996], respectively). We repeatedly observed 14 adult male territory holders in this population over several weeks to obtain extensive data on the advertisement displays produced by each focal male, the ambient temperature at a male's perch site, and the number of adult male neighbors (display recipients) that were active in the surrounding environment each time a male was observed. Since this species is a known thermoconformer (Hertz et al. 1993), it is likely that the ambient air temperatures measured at each male's location were similar to its body temperature. This combination of published and field collected data allowed us to generate predictions about relationships between display rates and temperature that were specific for this population, and to compare those predictions to the relationship between display rates and temperature observed in individuals of this population.

Both the genus-level analyses of Jamaican and Puerto Rican taxa, and the within-population analyses specific to *A. gundlachi*, required estimates of the "contextual reaction norms" of display rate as a function of ambient air temperature. A contextual reaction norm describes how a given behavior (here, display rate) immediately changes in response to variation in some environmental variable (e.g., temperature; see Stamps and Groothuis [2010] and Stamps [2016] for general discussions of contextual vs. other types of behavioral reaction norms and Ord et al. [2016a] for details specific to *Anolis* display behavior). We have previously shown that there are 2 ways to estimate the contextual reaction norms of *Anolis* advertisement displays. First, the contextual reaction norm for a given population can be approximated based on single observations of different individuals from that population

(Ord et al. 2010a). Second, the contextual reaction norms of individual lizards can be computed directly by repeatedly surveying each individual across a wide range of environmental conditions (Ord et al. 2016a). We adopted both approaches in this study, using the first for the genus-level analyses, and the second for the study of the *A. gundlachi* population.

## MATERIALS AND METHODS

### Data

Display data for 11 Puerto Rican taxa (8 species) and 5 Jamaican taxa (4 species) were taken from the data archive of Ord et al. (2010b). Free-living adult males were video recorded for periods of 20–30 min (mean  $\pm$  standard deviation [SD]:  $21 \pm 5$  min) using a digital camcorder mounted on a tripod. Males were considered to be territory holders if they performed at least one advertisement display within the first 10 min of recording. If a male failed to display within this time, the recording ceased and the researcher moved on to another adult male. Video recordings of focal males were used to quantify display rate, measured as the average number of display bouts performed per minute. Bouts were defined as any display movement separated by at least 3 s (see Ord et al. [2010a] for details). Ambient air temperature was measured immediately following video recordings at the perch site where the first advertisement display was performed by each lizard. Temperature data were taken from the personal archive of the first author and are provided in the Dryad archive accompanying the current paper (Ord and Stamps 2017). The median number of males surveyed per taxa was 30 (range: 8–41; see Supplementary Table S1 for details).

Observations for the 14 adult male *A. gundlachi* were conducted near the El Verde Field Station following the procedures outlined in Ord et al. (2016a). Briefly, adult males were initially assumed to be territory owners if they performed an advertisement display during a preliminary 10-min observation period. Presumed territory owners were then captured and marked with color-coded bee tags for individual identification. Each focal male was then repeatedly observed several times a day over a period of about 4 weeks (median observation time: 15 h over 24 days; range: 3–17 h over 8–25 days; see Supplementary Table S2 for individual sample sizes). For each observation period, males were video recorded for 15 min, regardless of whether any displays were performed. Display rate was quantified from these videos in an identical fashion to Ord et al. (2010a). Ambient air temperature was measured immediately following each video recording at either the perch site of first display, or at the perch site where the lizard was seen at the start of the video recording if the male was not observed to display (see Ord et al. [2016a] for other procedural details). During video recording, the surrounding environment was carefully surveyed for the presence of potential receivers (specifically adult male neighbors). Neighboring males were only counted as potential display recipients if they might have been visible to the resident male (i.e., not obscured by some physical obstruction or located at distances greater than 10 m; the latter found to be an important threshold distance for adult male territorial holders to detect a displaying male conspecific in robot playback experiments [Ord and Stamps 2008]; see also visual perceptual ranges computed in Ord [2012]). Data on display rates and recipient numbers were not reported in Ord et al. (2016b) and were taken from the personal archive of the first author and are provided in Ord and Stamps (2017); data on temperature was taken directly from the public data archive of Ord et al. (2016b).

### Statistical analyses

All analyses were performed using R version 3.2.3 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria). The first set of analyses assessed whether the performance or metabolic models were able to predict the slope of the contextual reaction norm of display rate versus temperature for *Anolis* taxa living in a range of thermal environments. The second set of analyses tested predictions from the performance, metabolic, and recipient models that were specifically parameterized for the El Verde population of *A. gundlachi*. In both cases, we used maximum-likelihood random regressions implemented in the “lme4” package ver 1.1-8 (Bates et al. 2015). These regressions were used to obtain both the predicted and observed trends across *Anolis* taxa (genus-level analyses) or across adult males for the El Verde population of *A. gundlachi* (within-population analyses). For genus-level analyses, models were based on a Gaussian error distribution (data approximated a normal distribution). These analyses did not incorporate the phylogenetic relationships of taxa because we were not able to find a method that implemented the type of complex statistical structure required for our purposes. Instead, we relied on the implicit assumption that lizards were free to vary their display rates as a function of temperature independently of phylogeny. For the within-population analysis of *A. gundlachi*, random regressions were based on a Gaussian or Poisson error distribution depending on the dependent variable examined (display rate or recipient number, respectively).

### Genus-level tests of the performance and metabolic hypotheses

#### Performance model

To estimate the shape of the relationship between performance and temperature, we used a variety of sources to compile the available data on maximum sprint or jump speed for *Anolis* species. These data were all estimates of maximal performance measured in a laboratory setting and took one of 3 forms (see also Supplementary Table S3): 1) raw data of performance speed for individual lizards tested at a range of different body temperatures for one or more populations obtained from the Dryad Digital Repository or provided directly by a study's authors (total of 9 taxa: 3 species, with 1–7 populations per species); 2) mean performance speed estimated for a sample of lizards tested at a range of different body temperatures obtained from the Dryad Digital Repository (2 taxa: 2 species, 1 population each); or 3) mean performance speed estimated for a sample of lizards tested at a range of different body temperatures extrapolated electronically from figures presented in published papers (1 taxa: 1 population of 1 species).

The first step was to standardize performance data by converting values to  $z$ -scores. This was necessary in order to directly compare the predicted shape of the thermal performance curve with the observed shape of display rate as a function of temperature. The conversion was made by computing the mean and SD of performance values across the temperatures tested by a study and for a given entity (either across an individual lizard for data of type 1 [see above] or across the mean estimates of the sample of lizards tested for data of type 2 and 3). The mean was then subtracted from each of the performance values, and this new value divided by the SD.

Next, a random regression was applied to the  $z$ -scores to estimate the relationship between performance and temperature across *Anolis* species. Thermal performance curves are often

modeled using a complex asymmetric function in which separate equations are built for the left (upward) and right (downward) side of the curve (e.g., Gunderson and Leal 2012). In order to simplify the process, while also allowing the inclusion of random effects (which were essential for all analyses), we applied a quadratic function to estimate a single, parabolic performance curve (NB: a quadratic expression still provides a reasonable estimate of the performance curve relative to other functions; see Angilletta [2006]). This quadratic function included 2 random effects: a random intercept and slope for individual identity to accommodate the repeated measures of individual lizards for some taxa (data of type 1; see above), and a random intercept and slope for taxon identity to account for potential differences among populations and species (relevant for all data types).

From this quadratic random regression, we used the 95% confidence intervals (CIs) of the upward slope (left side of the performance curve) and downward slope (right side of the performance curve) for direct comparison with the observed relationship between display rate and temperature (see below). For ethical reasons, performance studies usually test lizards over cool to moderately hot temperature ranges (see Supplementary Table S3) and rarely include the hottest temperatures that result in a rapid decline in performance. This meant our estimate of the upward side of the thermal performance curve could be derived with some confidence, but the statistical power for estimating the downward slope of this curve was lower because of limited empirical data at the hottest temperatures.

In order to compare the observed relationship between display rate and temperature to that of the maximal performance model, we converted field collected display rates to a  $z$ -score by subtracting the display rate of each lizard by its taxon mean and dividing this value by the taxon SD (8 males of the total 437 males sampled were removed as outliers prior to  $z$ -score conversion based on Chauvenet's criterion; Taylor 1997; see Supplementary Table S1). A quadratic random regression across taxa was then applied to obtain a genus-level contextual reaction norm of display rates ( $z$ -scores) as a function of ambient air temperature. This regression included a random intercept and slope for taxon identity to accommodate the potential for reaction norm differences among populations and species. The 95% CIs from the upward and downward slope were then compared directly with those predicted by the maximal performance model.

### Metabolic model

RMR varies as a function of both body size and body temperature. Published data on the relationship between RMR and temperature were based on lizards of a wide range of body sizes—including juveniles, adult females, and adult males—that were tested at one or more body temperatures. Since in this study we were specifically concerned with adult males, for each published metabolic study that we could find for *Anolis* (6 taxa: 3 species, with 1–3 populations per species; Supplementary Table S4), we first computed the mean body mass of the adult males tested in each taxon (in grams) and used this to estimate the mass-adjusted RMR at a given temperature for a lizard of that mass. This was done using the regression equation of RMR on mass at a tested temperature that was reported by a study or extrapolated from the trend line of this regression depicted in figures. For example, Kolbe et al. (2013) tested *A. sagrei* lizards of a wide range of body masses (<1.0 to ~10 g) from 3 different populations at 4 body temperatures (25 °C, 29 °C, 33 °C, and 37 °C) and for each population computed separate equations

of RMR as a function of body mass for each of those 4 temperatures. We used the mean adult male mass of the lizards tested (e.g., 5.0 g for one of the populations examined) to estimate 4 RMR values for that mass at each of the 4 temperatures. This approach was repeated for all of the available *Anolis* taxa.

We then applied the theoretical framework outlined by Gillooly and Ophir (2010) and natural-log-transformed mass-adjusted estimates of RMR and converted the associated body temperatures to degrees Kelvin ( $T$ ), which was then multiplied by Boltzmann's constant ( $k$ ,  $8.62 \times 10^{-5}$  eVK $^{-1}$ ) and inverse transformed ( $1/kT$ ). lnRMR was subsequently regressed on this temperature conversion using a random regression with a random intercept and slope for taxon identity. The 95% CIs of the slope was then used as the predicted relationship of display rate as a function of temperature under the metabolic model.

To obtain the estimate of the observed relationship between display rate and temperature that could be compared directly with the metabolic prediction, we first converted field collected display rates to bouts per second (following Gillooly and Ophir 2010) and used Gillooly and Ophir's function,  $\ln(rM^{1/4})$ , to standardize display rates by the mean body mass (in grams) of the adult males in each of the 16 *Anolis* taxa. Data on mean body mass were available for most taxa from the personal archive of the first author and are available in Ord and Stamps (2017). For 4 taxa in which this was not the case, data on adult male body mass were obtained from other sources (*A. cooki*: Janssen et al. 1984; *A. poncensis*, *A. pulchellus*, and *A. sagrei*: Losos JB, unpublished data; NB: the range of body masses of species examined in metabolic studies were similar to those of the 16 Jamaican and Puerto Rican *Anolis* examined for display rate: 2.7–6.6 g vs. 1.5–8.7 g, respectively). The associated temperature at which lizard display rates were measured was converted in the same fashion as those for the metabolic prediction (i.e., to  $1/kT$ ). Mass-adjusted ln-display rate was then regressed on this temperature conversion using a random regression with a random intercept and slope for taxon identity. The level of overlap between the computed 95% CIs of the slope from this reaction norm and those from the predicted slope were used to evaluate the similarity between the 2 slopes (predicted and observed).

### Within-population tests of the performance, metabolic, and recipient hypotheses for *A. gundlachi*

#### Performance model

Estimation of the maximal performance curve for the El Verde population of *A. gundlachi* was comparable to that of the genus-level analyses, with one exception. While the performance model predicts a parabolic (e.g., quadratic) relationship with temperature over a wide temperature range, the habitat occupied by the El Verde population of *A. gundlachi* was relatively cool by the standards of most anoles. The performance curve was therefore restricted to the left (upward) side of the curve, and preliminary analyses showed a close to linear increase in performance over the field temperatures typically experienced by these lizards when performing territorial advertisement displays (22 °C–30 °C).

The performance data we used were based on laboratory measures of maximal sprint speed data for 12 adult male *A. gundlachi* lizards from the El Verde population provided by Alex Gunderson (see also Gunderson and Leal [2016]). These sprint speed data were converted to  $z$ -scores and analyzed as a linear function over the temperatures that were the most similar to the range over

which territorial displays were observed in the field (22 °C, 27 °C, and 32 °C; see Supplementary Table S5). The random regression applied included a random intercept and slope for lizard identity. The 95% CIs of the slope was used as the predicted performance relationship for the males in this population.

To compute the observed display rate contextual reaction norm for males from the El Verde population, we first converted display rate data for each of the 14 adult males to  $z$ -scores and entered these into a linear random regression with a random intercept and slope for lizard identity. The computed slope from this reaction norm was then compared to that predicted by the performance model (see previous paragraph) using the level of overlap between the slope 95% CIs.

### Metabolic model

Estimation of the relationship between RMR and temperature followed the same procedure outlined for the genus-level analysis. RMR values were extrapolated from the metabolic equations estimated under laboratory conditions for adult male *A. gundlachi* from the El Verde population published by Rogowitz (1996). In this study, RMR as a function of body mass was measured for juvenile and adult males at either 15 °C or 30 °C. We used the mean body mass of the males in this study (6.6 g) to obtain 2 RMR values for a male of this size. These data were then natural-log transformed and regressed on the conversion of each temperature value ( $1/kT$ ). Because the slope from this regression was based on only 2 temperatures, it was not possible to compute 95% CIs for this slope (Supplementary Table S6).

Field collected display rates were mass-adjusted based on the size of each of the 14 adult males using the same function applied in the genus-level analysis ( $\ln[zM^{1/4}]$ ) (NB: the mean mass of adult males tested in the metabolic study of Rogowitz [1996] was within the range of adult male masses examined for display rate: 6.6 g vs. 6.3–10 g, respectively). Mass-adjusted display rate was then regressed on temperature ( $1/kT$ ) using a random regression that included a random intercept and slope for male identity. We then evaluated the level of overlap between the 95% CIs of this slope and the slope predicted by the metabolic model.

### Recipient model

The recipient model is based on 2 assumptions: 1) the number of potential recipients is related to ambient temperature and 2) display rate is related to the number of potential recipients. To reveal the underlying relationships between temperature, recipient number, and display rate for the 14 male *A. gundlachi* lizards, we generated 5 alternative path models based on linear random regressions which included a random intercept and slope for male identity. Path models were developed using the “d-separation” approach outlined in Shipley (2009) in order to accommodate the multilevel structure of the analyses. The 5-path models considered the following scenarios (see Figure 4 for graphical representations). Model A was consistent with the recipient hypothesis in which recipient number is dependent on temperature, and males adjusted the number of advertisement displays based on the number of recipients in the surrounding environment and not as a direct function of temperature. Models B–D were consistent with the performance and metabolic models in which temperature has a direct physiological impact on display rate. Models C and E were partly consistent with the recipient hypothesis in that males adjust display rates according to the number of potential recipients in the environment but differs because recipient number is not dependent on temperature. More specifically:

Model A: Temperature has no direct effect on display rates, but it does affect the number of potential recipients and males adjust their display rates accordingly.

Model B: Temperature has a direct effect on both recipient number and display rate, but there is no direct effect of recipient number on the number of displays performed by males.

Model C: Temperature and recipient number both have a direct effect on display rate, but temperature does not affect recipient number.

Model D: Temperature has a direct effect on display rate, but not on recipient number, and males do not adjust display rates to recipient number.

Model E: Temperature has no effect on display rate and males adjust their display rates according to the number of recipients, which are not dependent on temperature.

For each of these models, a C-statistic was computed (Shipley 2009) and then converted into a second-order correction of Akaike's Information Criterion value,  $AIC_c$ , based on formula presented in Shipley (2013). The model with the lowest computed  $AIC_c$  value is considered to be the best-supported model (Burnham and Anderson 2002). However, we report these values as  $\Delta AIC_c$ , which is the lowest value of this best-supported model subtracted from each model's computed  $AIC_c$  value. Those models within 2  $AIC_c$  units of the best-supported model (i.e.,  $\Delta AIC_c \leq 2.0$ ) are generally considered to be equally compelling candidate models to the best-supported model (which has a  $\Delta AIC_c$  of 0.0). We also illustrate the effect size of assumed causal links in each model using  $t$ -values computed for the associated predictor slopes.

## RESULTS

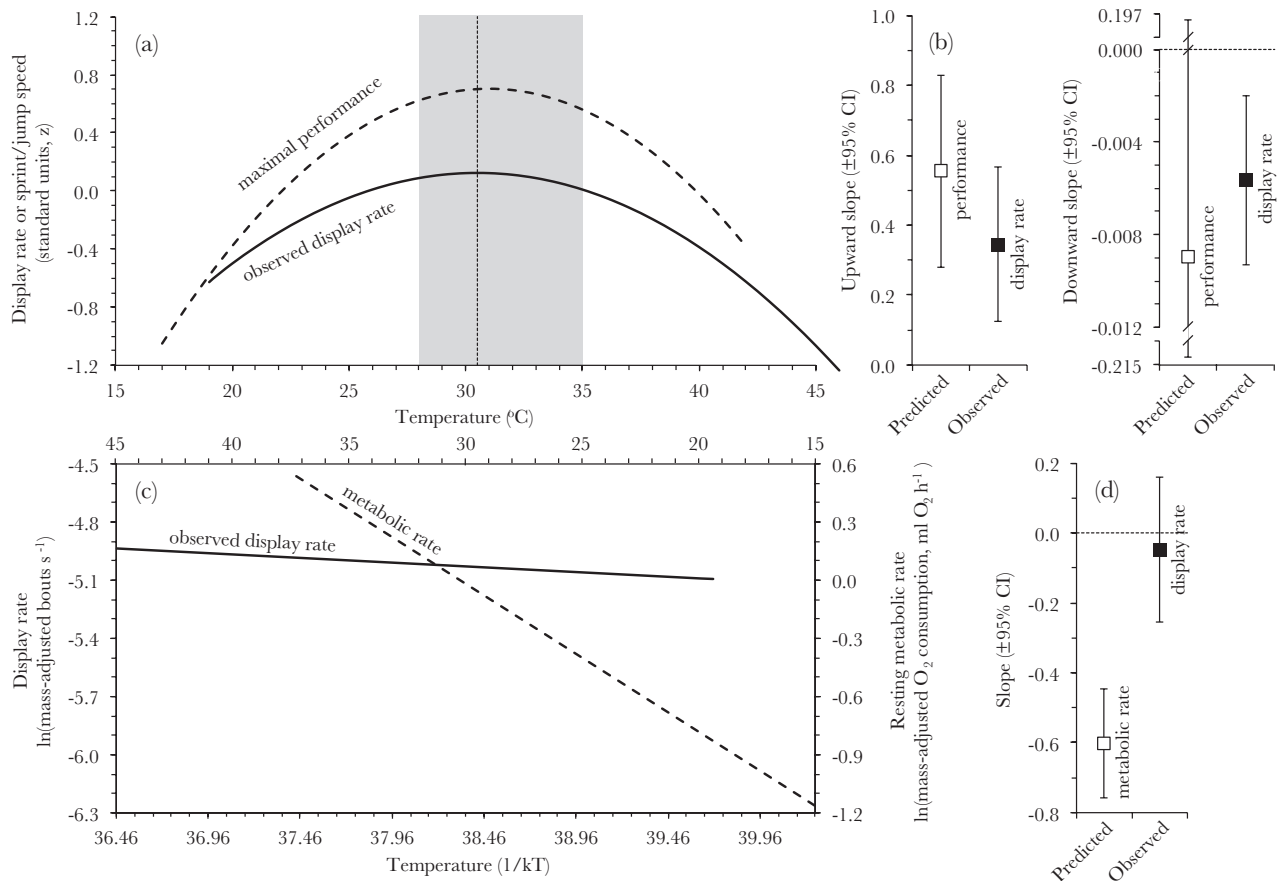
### Genus-level contextual reactions norms for display rates as a function of temperature

The quadratic function applied to standardized display rate observations for males of the 16 Jamaican and Puerto Rican taxa exhibited a clear concave relationship with ambient temperature (Figure 2a; further elaborated in Supplementary Figures S1a and S2a). It had an upward and downward slope statistically indistinguishable from the shape of the performance model generated from published data on maximal sprint or jump speed for a variety of anoles (Figure 2b; Supplementary Table S3). Moreover, the inferred peak for display rates for the 16 taxa occurred at a temperature (31 °C) that was well within the range of the temperatures reported for peak locomotor performance in anoles (mean 33 °C, range 28 °C–35 °C; Figure 2a).

In contrast, there was little support for the metabolic model. There was no overlap between the slope of mass-adjusted display rate with temperature for the 16 taxa and the predicted slope computed from mass-adjusted RMRs generated from published data on a range of anoles (Figure 2c, d; Supplementary Table S4; see also Supplementary Figures S1b and S2b).

### Within-population contextual reaction norms of *A. gundlachi*

The reaction norm of the standardized display rates of the 14 adult male lizards increased as a linear function of ambient temperature (Figure 3a; further elaborated in Supplementary Figures S3a and S4a) and in a fashion that was virtually identical to that predicted by the performance model parameterized using the maximal



**Figure 2**

Observed contextual reaction norm of territorial display rate as a function of ambient temperature (solid line) inferred across adult male Puerto Rican and Jamaican *Anolis* lizards compared to the predicted trends (dashed line) under the (a, b) maximal performance hypothesis and (c, d) metabolic rate hypothesis. The gray area in (a) highlights the range of temperatures that maximal performance has been reported in *Anolis* lizards, while the dotted vertical line indicates the temperature corresponding to the apex of the display rate reaction norm. Plots in (b, d) compare the computed “on-average” (main effect) slopes of the predicted trends versus observed reaction norm of display rate (which are graphically illustrated in a and c).

sprint speed of adult males from the same population (Figure 3b; Supplementary Table S5).

There was also some support for the metabolic model. The slope of the relationship between display rate and temperature across the 14 lizards was statistically comparable to the slope predicted by the metabolic model derived from published data on adult males from this same population (i.e., 95% CIs overlapped; Figure 3c, d; Supplementary Table S6). However, the slope of the display rate reaction norm was somewhat steeper than expected under the metabolic model (Figure 3d, further elaborated in Supplementary Figures S3b and S4b).

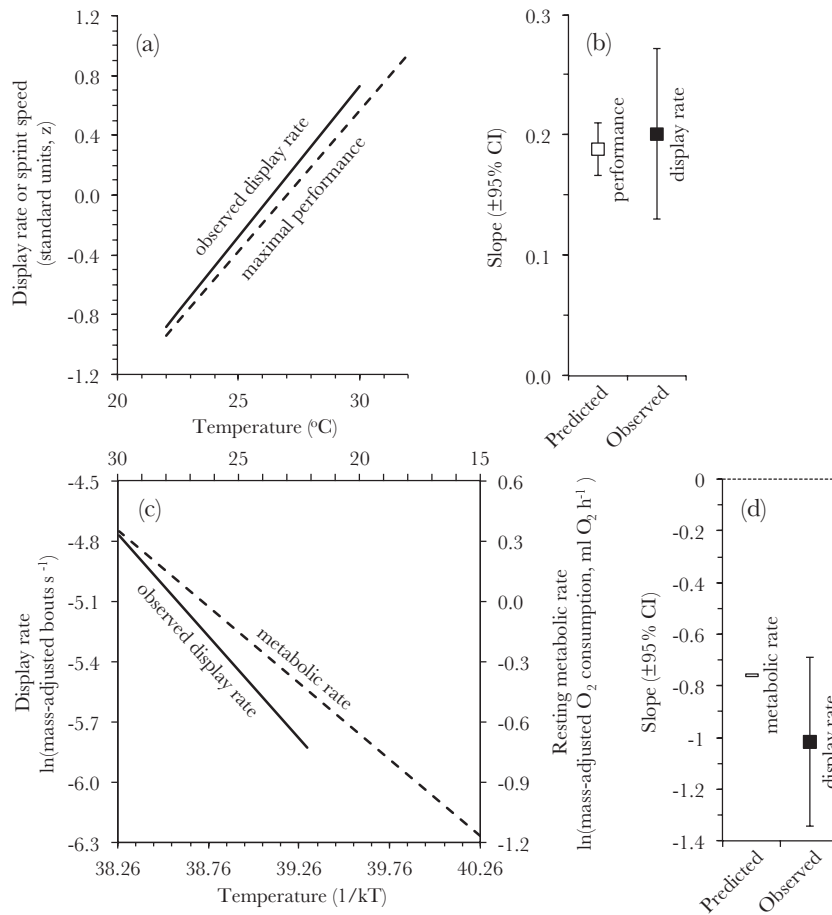
Finally, there was no support for the recipient model. The best-supported path model by a clear margin was one that assumed ambient temperature had a direct effect on both display rate and recipient number, but that males did not adjust their display rates according to the number of potential recipients active in the environment (Model B; Figure 4).

## DISCUSSION

The display rate reaction norms of *Anolis* male lizards were clearly dependent on ambient temperature in a manner that was consistent with predictions from Gunderson and Leal’s (2015) performance

model. In all of our analyses, the observed relationships between display rates and temperature were comparable to those predicted on the basis of a model derived from data on thermal performance curves previously reported for *Anolis* lizards (Figures 2a and 3a; Supplementary Tables S3 and S5). Although the metabolic model (Gillooly and Ophir 2010) could not be rejected entirely, it failed to predict the relationships between display rate and temperature in male lizards for *Anolis* populations observed over a wide range of field temperatures (Figure 2c, d; Supplementary Table S4). In addition, for *A. gundlachi*, the observed slope of display rates as a function of temperature tended to be steeper than the slope predicted by the metabolic hypothesis (Figure 3c, d; see also Supplementary Figure S3b). There was no support for the recipient model. Although the number of potential recipients around individual male *A. gundlachi* did change as a function of ambient temperature, there was no indication that males adjusted their display rates based on the number of potential recipients around them at the time they gave their displays (Figure 4).

To our knowledge, this is the first time that anyone has formally tested multiple hypotheses to explain observed relationships between signal rates and temperature in ectotherms. Our results support the hypothesis that in *Anolis* lizards at least, the same factors that constrain maximal performance as a function of temperature



**Figure 3**

Observed contextual reaction norm of territorial display rate as a function of ambient temperature across 14 adult male *A. gundlachi* lizards compared to predicted trends (dashed line) under the (a, b) maximal performance hypothesis and (c, d) metabolic rate hypothesis parameterized using published data on males from the same population (Rogowitz 1996; Gunderson and Leal 2016). Plots in (b, d) compare the computed “on-average” (main effect) slopes of the predicted trends versus observed reaction norm of display rate (which are graphically illustrated in a and c).

also constrain the rate of production of communication signals as a function of temperature. The ultimate outcome is that lizards appear to perform, on average, as many territory advertisement displays over a given timeframe as their temperature dependent physiology generally allows. In turn, this pattern is probably adaptive because it results in higher display rates during periods when more recipients are likely to be around to observe them (see discussion of recipient model below).

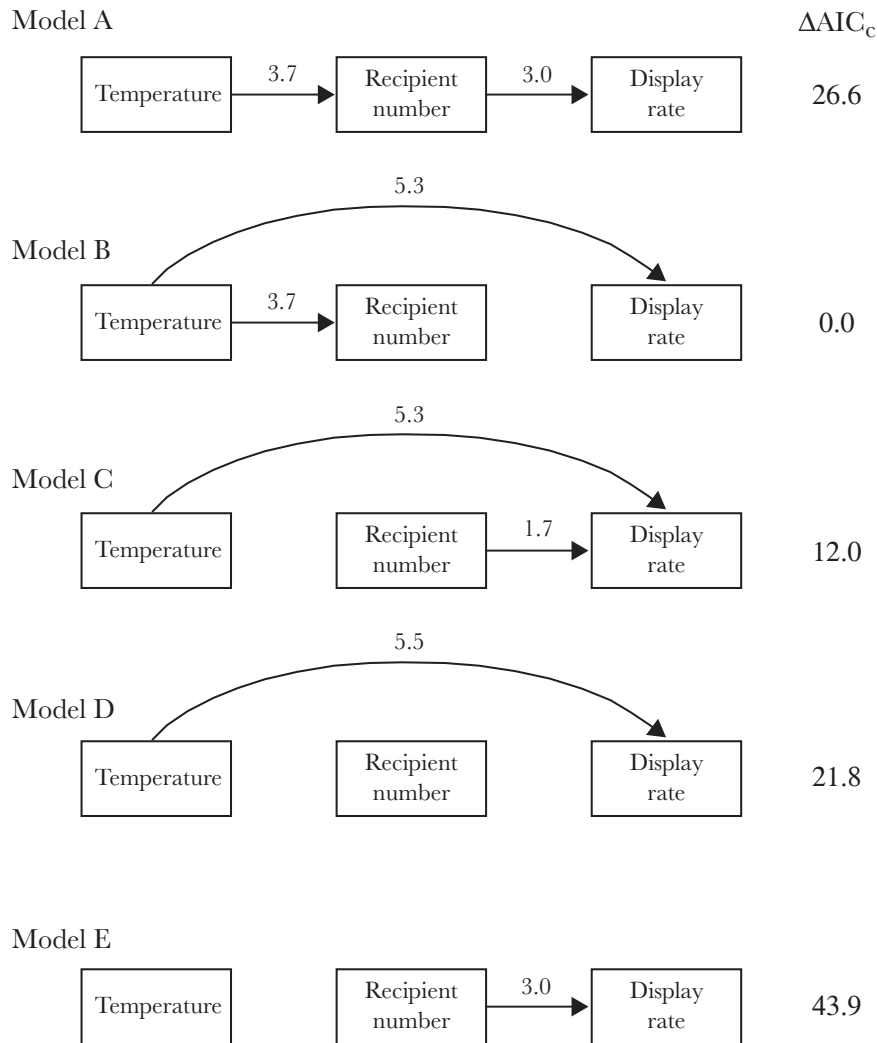
Interestingly, when Gunderson and Leal (2015) tested their performance model using empirical data from an anole (*A. cristatellus*), their results were largely unresponsive of their general predictions. We suspect that this might have occurred because the authors used the performance model to estimate the relationship between “activity rate” and temperature. Activity rate was estimated by combining observations of a wide range of behaviors, including the proportion of time spent feeding, mating, fighting, and performing territorial displays. However, combining a diverse range of behaviors into a single metric of activity ignores the possibility that different types of behavior might involve different levels of exertion or stamina. By restricting our analyses to a single type of behavior—the production of advertisement displays—and to a type of behavior that always requires strenuous physical activity and lasts for a limited amount of time (as do bursts of maximal locomotor speed), we

were able to show that the observed contextual reaction norms for display rate as a function of temperature were remarkably similar to those predicted on the basis of the thermal performance curves of *Anolis*.

The alternative physiological model of temperature-dependent, mass-specific metabolic rate (Gillooly and Ophir 2010) was an exciting advance in communication theory. As originally formulated, it focused on explaining broad-level (interspecific, inter-taxa) variation in the production and structure of acoustic signals based on the energetic constraints imposed by the metabolism of those species (Gillooly and Ophir 2010; Ophir et al. 2010). Given the production of vocalizations and the physical movements used in many visual displays are both dependent on neuromuscular activity and energetically costly to produce, the metabolic model should be equally applicable to taxon-level variation in rates of dynamic visual displays.

We are aware of only one study that has attempted to apply the metabolic model to variation in signal rates within a single species. Ziegler et al. (2016) examined call rate among male treefrogs (*Hypsiboas pulchellus*) as a function of temperature and concluded that the observed slope of  $-0.45$  for that population was inconsistent with the predicted slope of  $-0.65$  obtained from Gillooly and Ophir (2010). However, this predicted slope of  $-0.65$  was based on





**Figure 4**

Model support from path models depicting various alternative scenarios of the relationships among temperature, recipient number and territorial display rate for 14 adult male *A. gundlachi*. Values above connecting arrows are *t*-scores; those greater than 2.0 are considered to be statistically distinguishable effects from zero. The recipient hypothesis corresponds to Model A.

the general scaling relationships of metabolic rate with temperature extrapolated across a diverse range of ectotherms (Gillooly et al. 2001). When Ziegler et al.'s (2016) observed slope is compared to one specifically derived for amphibian metabolic rate,  $-0.47$  (see Gillooly et al. [2001]), the call rates of male frogs do in fact appear to match the predictions of the metabolic model quite well. This suggests the metabolic model may still be useful for predicting variation in signal production among individuals within species, despite our study providing only limited evidence for the production of dynamic visual displays in anoles.

Finally, our results failed to support the recipient model because we found no support for the hypothesis that *A. gundlachi* lizards directly modified their display rates based on the number of neighboring territorial males that were visible at the time focal lizards gave their advertisement displays. We suspect that under natural conditions, territory owners might have difficulty accurately assessing the number of potential recipients around them at a given moment because of cognitive limits, the cryptic nature of those recipients, or obstacles in the environment. However, our results also indicate that territorial males did have access to a reliable

indirect cue to the number of potential recipients: ambient temperature was positively related to the number of observed neighbors surrounding a territorial male (Figure 4). Hence, any male who was able to assess the current ambient temperature would also have a reasonable estimate of the current number of potential recipients for his advertisement displays.

Given the many reports of relationships between activity rate and temperature in other ectotherms (see Introduction), we suggest that other ectotherms might also be able to use ambient temperature as an indirect cue to the number of potential recipients for their advertisement signals. That is, to the extent that it is adaptive for ectotherms to track the number of potential recipients in the local environment, they might be able to rely on the indirect cue of ambient temperature, as opposed to the cognitive and sensory challenges of attempting to directly assess the number of potential recipients in the vicinity at any given moment.

We anticipate that the general framework applied in the current study of combining published laboratory data with field-based observational data on the rate of signal production should be possible for a range of other ectotherms. While early studies

of ectotherm communication were often focused on the potential cause of temperature-dependent signal rates (e.g., Walker 1975), studies today usually only consider temperature as a covariate to include in statistical analyses rather than a phenomenon requiring exploration in itself. We hope the application of the framework developed here will provide new motivation and new opportunities for investigating the physiological mechanisms that underlie temperature-dependent signaling in ectotherms, and the potential that signalers might be capable of using ambient temperature as an indirect cue of receiver availability.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* Online.

We are especially grateful to Grace Charles and Meredith Palmer for their help in the field on the original longitudinal study of *Anolis gundlachi* territorial behavior. We would also like to thank Jonathan Losos for sharing his data on *Anolis* body mass, and Lisa Schwanz for comments on an early version of this paper.

Data accessibility: Data used are publicly available in the following Dryad Digital Repository archives: Ord et al. (2010b; doi:10.5061/dryad.1619), Ord et al. (2016b; doi:10.5061/dryad.td1g2), and Ord and Stamps (2017; doi:10.5061/dryad.f06rn).

**Handling editor:** John Fitzpatrick

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