

Natural History Note

Dawn and Dusk “Chorus” in Visually Communicating Jamaican Anole Lizards

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ABSTRACT: A key hypothesis explaining the existence of dawn and dusk choruses in acoustically communicating animals centers on the need to advertise continued territorial occupancy after and before a period of nocturnal inactivity. If this hypothesis is correct, it follows that similar dawn and dusk choruses should occur in territorial animals exploiting other signal modalities. Adult male *Anolis* lizards defend territories by using elaborate head-bobbing displays and extensions of a throat fan or dewlap. Males are inactive at night and return to their territories at dawn, remaining there until dusk. I quantified the production of visual displays as a function of time of day for four species on the island of Jamaica: *Anolis lineatopus*, *Anolis sagrei*, *Anolis grahami*, and *Anolis opalinus*. All exhibited dawn and/or dusk peaks in display behavior. These patterns have remarkable parallels with the dawn and dusk choruses reported for many acoustically communicating animals.

Keywords: animal communication, dawn/dusk chorus, diel patterns, territory behavior, *Anolis*.

The dawn chorus of singing birds is one of the most evocative and familiar phenomena of the natural world. Why birds and other acoustically communicating animals (e.g., primates, frogs, and insects; see references in Staicer et al. 1996) should concentrate their calling effort early in the morning is still not clear. There are a number of non-

mutually exclusive hypotheses, ranging from intrinsic (e.g., circadian cycles in energy reserves; Barnett and Briskie 2007) to environmental (e.g., favorable atmospheric conditions at dawn that facilitate the transmission of animal sounds; Henwood and Fabrick 1979; Brown and Handford 2003), but the most persuasive hypothesis suggests a social function behind increased signaling at dawn (reviewed by Staicer et al. [1996] and Burt and Vehrencamp [2005]). In particular, empirical evidence for many birds suggests that heightened dawn signaling serves in territory defense (e.g., Amrhein et al. 2004; Burt and Vehrencamp 2005; Kunc et al. 2005; Liu and Kroodsmas 2007). As residents return to their territories after a period of inactivity, they broadcast to neighbors their continued territorial occupancy, leading to a peak in signal output at dawn (Staicer et al. 1996; Burt and Vehrencamp 2005). It also follows that similar bursts in signal production will tend to occur at dusk (Staicer et al. 1996, following Young 1981) as residents seek to reinforce territorial ownership before moving off territories for the night. Considering that territorial defense is an integral aspect of the behavior of many animals, the dawn and dusk “choruses” might not be limited to acoustically communicating animals. In principle, the phenomenon should be equally applicable to territorial signals using other sensory modalities.

Visually communicating diurnal *Anolis* lizards are one system in which this might be the case. At least two aspects of anole behavioral ecology suggest this. First, male Caribbean anole lizards mediate territorial disputes and advertise continued presence on a territory through the production of headbobs that are often accompanied by the extension and retraction of a colorful throat fan or dewlap (a video is available in the online edition of the *American Naturalist*). Only when exchanges of these visual displays fail to resolve disputes do males resort to physical combat. When they occur, fights are prolonged (e.g., 40 min or more; T. J. Ord, personal observation) and violent biting/sparring matches that can send one or both combatants falling from their perches. Visual displays are therefore a vital part of an adult male’s territorial behavior. Furthermore, male territories overlap those of one or more females

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(Stamps 1983). The maintenance of territory boundaries against incursions from other males is consequently paramount for a resident male to monopolize access to females (Rand 1967; Jenssen et al. 1995). Second, *Anolis* lizards are generally inactive at night and sleep among vegetation that is away from their diurnal territories (e.g., Singhal et al. 2007). On returning to display perches at the start of each day, lizards must reestablish territorial ownership by advertising continued occupancy to neighbors, in much the same way as territorial birds (e.g., Liu 2004). This predicts early morning peaks in territorial display. We might also expect increases in territorial activity at dusk (e.g., Kloubec and Capek 2005) to reinforce territory ownership before moving to sleeping sites.

I examined whether dawn and dusk correspond to marked increases in display activity by quantifying the behavior of adult male lizards for four diurnal *Anolis* species on the island of Jamaica (see fig. A1 in the online edition of the *American Naturalist*). My prediction was that the increased need to advertise territorial ownership at these times will in turn produce spikes in signal production. I also tested two alternative hypotheses that might lead to similar diel patterns in display. First, although cooler morning and evening temperatures in the tropics are not generally expected to restrict activity in these ectotherms (e.g., Rand 1964), hotter midday temperatures could result in reduced display activity as animals devote more time to thermoregulation (e.g., Hertz 1992). Second, lizards might compensate for lower light levels at dawn and dusk by displaying more at these times to ensure that neighbors readily detect signals. In both cases, peaks in display production would also be expected to occur at dawn and dusk. To distinguish between the general effect of time of day and that of temperature or light, I compared the relative influence of these factors on temporal variation in display activity, using effect sizes calculated within multiple-regression models.

Material and Methods

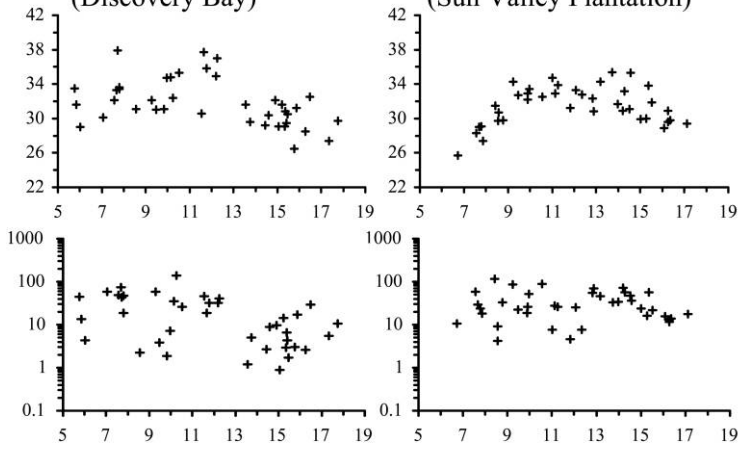
To evaluate the generality of potential diel patterns in display behavior, I replicated my observations across species pairs for two ecologically distinct ecomorphs (see Williams 1983): “trunk-ground” *Anolis lineatopus* and *Anolis sagrei* and “trunk-crown” *Anolis grahami* and *Anolis opalinus* (see

fig. A1). All observations were conducted in 2006 from May to June, which corresponds to the primary activity season of these animals, when males are aggressively defending territories. Observations of *A. lineatopus*, *A. grahami*, and *A. sagrei* were conducted on the north coast near the Discovery Bay Marine Laboratory (elevation 1–10 m; see fig. A2 in the online edition of the *American Naturalist*). I also conducted observations on a second population of *A. lineatopus* roughly 50 km east of Discovery Bay on a privately owned coconut plantation 5 km inland (elevation ~75 m). Finally, *A. opalinus* was observed at sites around Hardwar Gap and Hollywell Park (elevation 1200–1300 m) in the Blue Mountains on the southeastern side of the island near Kingston. While all species examined share a similar degree of territoriality, important distinctions exist in thermal ecology and habitat ambient light. For example, cooler temperatures are experienced by *A. opalinus* in the mountains relative to the hotter preferred temperatures of *A. sagrei*, with both of these species occupying brighter environments than the Discovery Bay population of *A. lineatopus* (see figs. 1, 2).

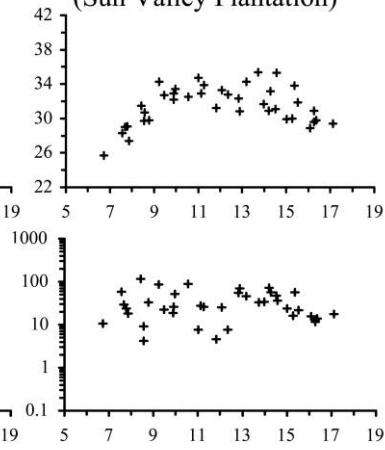
Adult males were the primary focus of this study because the mating system of anoles is centered on establishment and defense of territories by males. Lizards were located by quietly walking through the preferred habitat of each species. Individuals were generally found sitting on tree trunks, walls, or branches of large bushes. Once an adult male had been identified, I set up a digital camcorder (Panasonic GV-500) 5–6 m away from the lizard’s perch and videorecorded the behavior of the animal continually for 10 min. If lizards were observed to display during this period, I counted the number of neighboring adult males and females (the presence of which can be expected to influence display activity in focal lizards) and recorded several environmental variables as part of a separate study. These measures included temperature and ambient light. Temperature was measured with a digital thermometer at the site where animals were first observed to display. Habitat light was also measured at this site using an LI-250A portable light meter with an LI-190SA Quantum Sensor (both from LI-COR) positioned horizontal to the ground at the lizard’s eye level. Data collected were the average of estimates with the sensor pointing left and right, corresponding to light entering the left and right eye, respectively (e.g., see Fleishman et al. 1997). If animals failed to

Figure 1: Display activity in trunk-ground Jamaican anoles from dawn (0530 hours) to dusk (1830 hours): *A*, two populations of *Anolis lineatopus* observed at Discovery Bay and Sun Valley Plantation; *B*, a single population of *Anolis sagrei* observed at Discovery Bay. The top two plots illustrate temperature ($^{\circ}\text{C}$) and ambient light (\log_{10} , $\mu\text{mol s}^{-1} \text{m}^{-2}$) changes over time for each population and species. The bottom three plots depict total time spent (s) in each display type over a 10-min period. Solid regression lines of display activity on time of day include all animals, while dashed trend lines reflect those animals that displayed at least once. Arrows highlight extreme outliers identified by boxplot analysis of the subset of data for lizards observed to display. These points were included in the calculation of all trend lines shown.

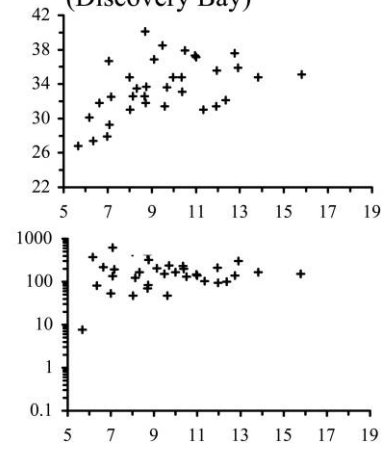
A *Anolis lineatopus*
(Discovery Bay)



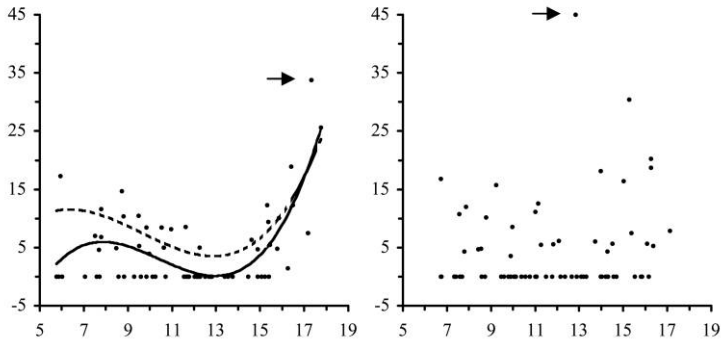
(Sun Valley Plantation)



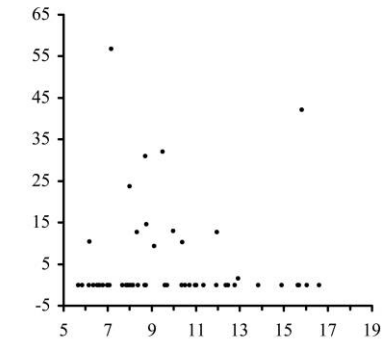
B *Anolis sagrei*
(Discovery Bay)



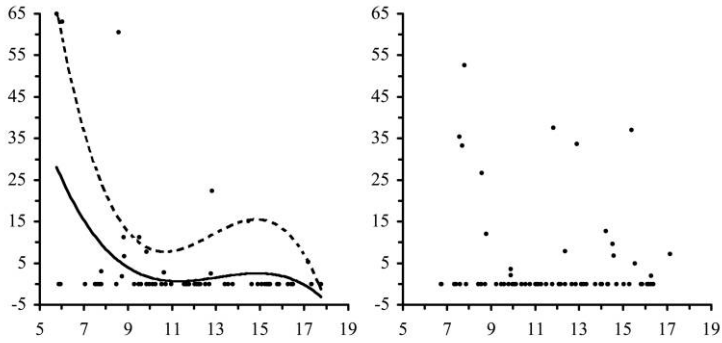
Headbobs



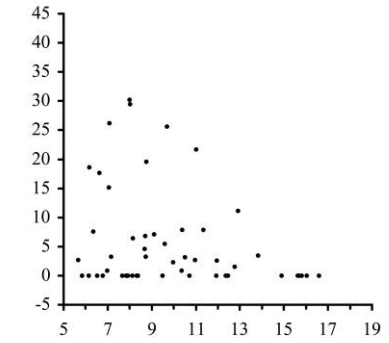
Headbobs



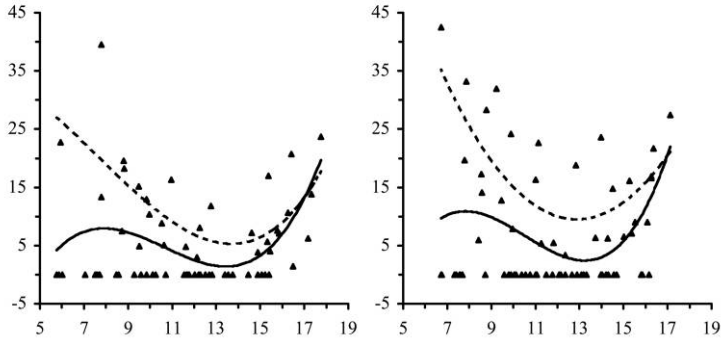
Stepbobs



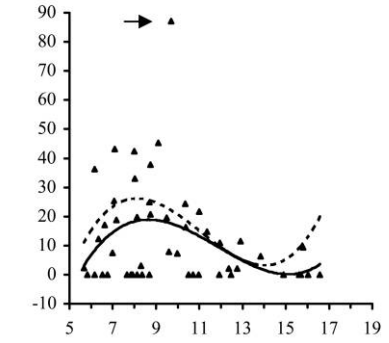
Headnodes



Dewlaps



Dewlaps



Time of day (24-hrs)

Time of day (24-hrs)

Time of day (24-hrs)

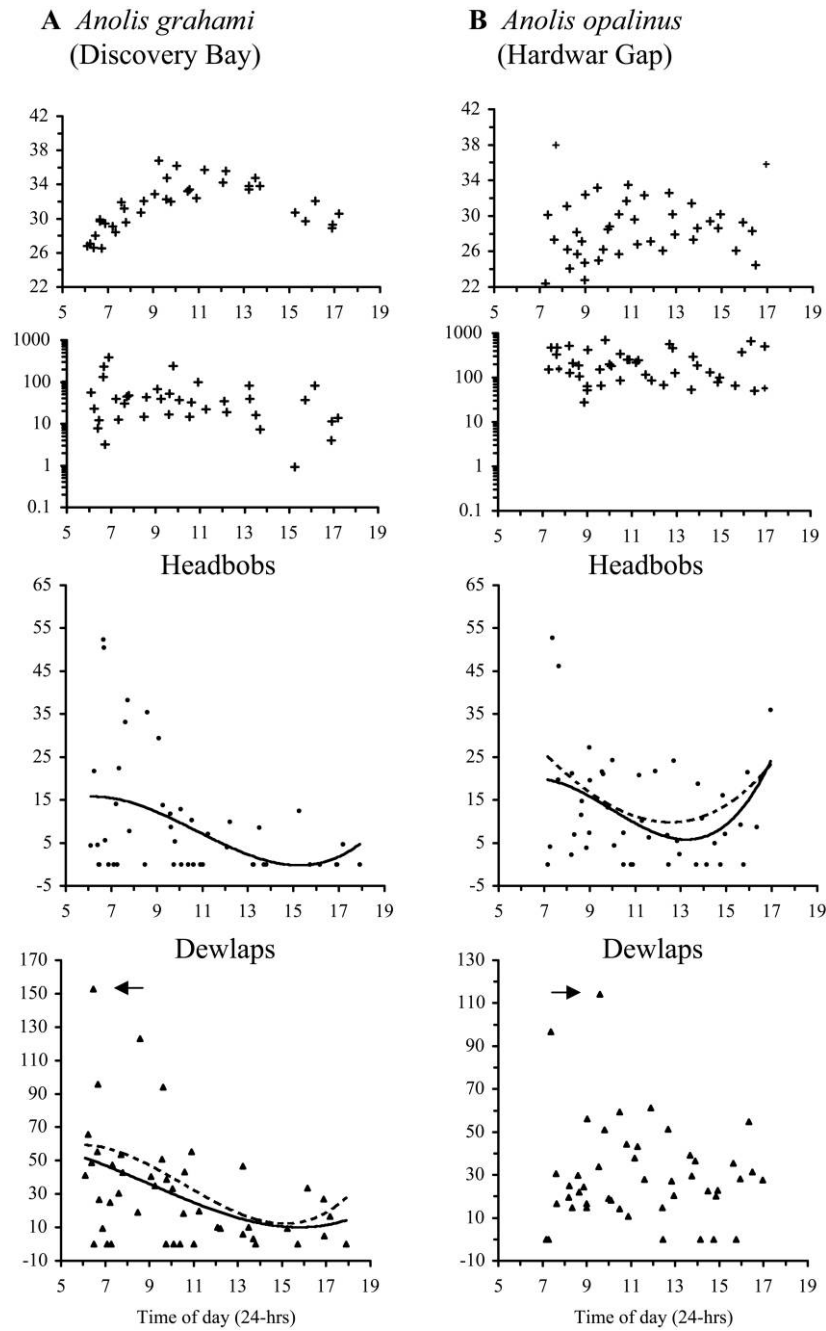


Figure 2: Display activity of trunk-crown Jamaican anoles from dawn to dusk. *A*, *Anolis grahami* observed at Discovery Bay. *B*, *Anolis opalinus* observed at Hardwar Gap in the Blue Mountains. See figure 1 for plot details.

display during this period, I noted only the time the trial was started. Each area was visited only once and explored systematically to ensure that animals were not inadvertently resampled. Surveys were conducted extensively throughout the day to ensure comprehensive and equal coverage of all time periods.

The total time spent performing displays over 10 min was scored blind from digital videos to the nearest frame (one NTSC video frame equates to 33 ms). Headbob and dewlap displays were analyzed separately, as were two other distinct display types produced by *A. lineatopus* and *A. sagrei* (“stepbobs” sensu Stamps 1973 and “headnods”

[shown in the video in the online edition] sensu McMann 2000, respectively). I considered these display types separately because they may differ in factors influencing their production. For example, displays used to advertise continued territory occupancy are expected to exhibit dawn and dusk peaks in production, whereas this may not be the case for displays employed as directed threat signals to individual intruders. At this stage, it is unclear which display types function as long-range, broadcast displays and which are directed, short-range threat displays.

I examined the distribution of observation times to confirm that animals were observed at all times of the day and that peaks in display production were not a reflection of failing to find animals during the hotter midday period. To assess display output, I used the fit of a cubic regression to evaluate the predictive value of time of day on the total time animals spent displaying over 10 min. Specifically, I predicted that display production would increase sharply and peak soon after dawn as individuals became active and peak again just before dusk. Boxplots of display activity for each species/population were inspected separately for outliers, and regressions were repeated with extreme values removed.

Finally, when an effect of time was detected on display activity, I repeated analyses for the subset of data where additional environmental data had been collected (i.e., when animals displayed). These multiple regressions included polynomials for time and additional linear terms for temperature ($^{\circ}\text{C}$), ambient light (\log_{10} , $\mu\text{mol s}^{-1} \text{m}^{-2}$), and number of nearby conspecifics (total number of adult male neighbors and females within 12 m). Terms that explained the least amount of variation were dropped sequentially from the model, with the criteria for remaining in the final model set at $P = .1$. All statistical analyses were conducted with SPSS, version 11.5 (SPSS, Chicago), for the Mac OS X operating system.

Results

Sunrise and sunset in May and June 2006 were approximately 0530 and 1830 hours, respectively. For all species, lizards were found soon after dawn and observed throughout the day. I continued to find animals until it became too dark to videorecord in the early evening (table 1; figs. 1, 2). The exception was *Anolis sagrei*. Sampling for this species occurred toward the end of June, which overlapped with the onset of the rainy season on Jamaica, and late afternoon storms tended to interrupt my evening observations.

Display activity varied considerably during the course of the day (table 2). All species generally exhibited a peak in display output soon after dawn and/or just before sunset. These patterns varied depending on the type of display,

Table 1: Observation times of Jamaican *Anolis* lizards

Species, location	Period sampled (days)	N	Time of day	
			Earliest	Latest
<i>A. lineatopus</i> :				
Discovery Bay	10	65	0546	1745
Sun Valley				
Plantation	6	67	0643	1707
<i>A. sagrei</i> :				
Discovery Bay	7	51	0540	1635
<i>A. grahami</i> :				
Discovery Bay	10	46	0606	1754
<i>A. opalinus</i> :				
Hardwar Gap	5	46	0710	1657

Note: Sampling for Sun Valley and Hardwar Gap are truncated by approximately 30 min because of extended commute times in the morning and evening to/from these locations.

with only *Anolis lineatopus* (a trunk-ground ecomorph; fig. 1) and *Anolis grahami* (a trunk-crown ecomorph; fig. 2) at Discovery Bay showing dawn or dusk peaks regardless of display type. *Anolis sagrei* and *Anolis opalinus* had morning and/or late afternoon bursts in production for only dewlap and headbob displays, respectively. The only important change with the removal of outliers highlighted in figures 1 and 2 was in the Sun Valley population of *A. lineatopus*, where a weak trend was subsequently detected between headbob display activity and time of day (see table 2).

In only two cases were factors other than time of day predictive of display activity. Multiple-regression analyses on displaying animals with factors for time, temperature, ambient-light level, and number of nearby conspecifics revealed that headbob display production tended to increase in *A. grahami* with temperature and, to some extent, number of nearby conspecifics, (overall model that includes time of day: $r^2 = 0.41$, $P = .002$; with a covariate for temperature: $r^2 = 0.17$, $b = 3.58$, $P = .02$; and with a covariate for conspecific number: $r^2 = 0.09$, $b = 3.60$, $P = .08$). There was also a weak, positive relationship between headbob displays and number of conspecifics in *A. opalinus* (overall model that includes time of day: $r^2 = 0.28$, $P = .007$; with a covariate for conspecific number: $r^2 = 0.08$, $b = 3.41$, $P = .07$). Importantly, time of day explained more variation in display production than temperature and/or the number of nearby adult conspecifics.

Discussion

This study shows that Jamaican anoles generally concentrate the production of their displays soon after dawn and/or just before dusk. This pattern is well defined for some display types and weak or absent for others, yet the reg-

Table 2: Diel patterns of display activity for Jamaican *Anolis* lizards shown by cubic-regression analysis

Species, location, display	All animals					Those that displayed				
	<i>N</i>	df	<i>r</i> ²	<i>F</i>	<i>P</i>	<i>N</i>	df	<i>r</i> ²	<i>F</i>	<i>P</i>
<i>A. lineatopus:</i>										
Discovery Bay	65	61								
Headbobs			.50	19.97	<.001 ^a	30	26	.45	6.94	.001 ^a
Outliers removed			.39	12.61	<.001 ^a			.34	4.20	.02
Stepbobs			.24	6.28	.001 ^a	14	10	.61	5.22	.02
Dewlaps			.18	4.53	.006 ^a	30	26	.38	5.38	.005 ^a
Sun Valley Plantation	67	64								
Headbobs			.04	1.41	.25	29	25	.03	.39	.68
Outliers removed			.10	3.32	.04			.07	.86	.44
Stepbobs			.02	.90	.41	18	14	.24	2.18	.15
Dewlaps			.11	4.00	.02 ^a	31	27	.39	8.74	.001 ^a
<i>A. sagrei:</i>										
Discovery Bay	51	47								
Headbobs			.04	.66	.58	13	9	.41	2.12	.17
Headnodes			.09	1.59	.21	29	26	.09	1.26	.30
Dewlaps			.13	2.39	.08	29	26	.22	2.48	.08
Outliers removed			.14	2.58	.07			.32	3.85	.02 ^a
<i>A. grahami:</i>										
Discovery Bay	46	42								
Headbobs			.18	3.00	.04	25	21	.20	1.77	.18
Dewlaps			.18	3.11	.04	36	32	.26	3.75	.02 ^a
Outliers removed			.16	2.66	.06			.27	3.83	.02 ^a
<i>A. opalinus:</i>										
Hardwar Gap	46	43								
Headbobs			.16	3.99	.03 ^a	38	34	.16	3.16	.06
Dewlaps			.01	.25	.78	41	37	.006	.10	.90
Outliers removed			.003	.06	.94			.006	.10	.90

Note: Results are presented for all animals observed and the subset of those that produced at least one display. See figures 1 and 2 for outliers. False discovery rate (FDR) threshold was calculated for eight comparisons for *A. lineatopus* and *A. sagrei* and six comparisons for *A. grahami* and *A. opalinus*.

^a *P* values that remain significant once the FDR has been controlled for following Benjamini and Hochberg (1995).

ularity of at least some display behavior exhibiting these peaks across all species examined is striking. Furthermore, no other factor accounted for this trend (e.g., temperature or light). These diel patterns are reminiscent of the spectacular dawn and dusk choruses of birds and other acoustically communicating animals. As is the case for these classic chorusing species, there are a number of reasons why anole lizards might concentrate the production of visual displays to particular times of the day.

Experimentally testing the territorial-defense hypothesis in the wild is difficult. The observations presented here are therefore particularly valuable because they document the chorus phenomenon in an entirely new signal modality and taxonomic group, adding general weight to the broad applicability of the territorial-defense hypothesis. Even so, if this hypothesis is indeed correct, bursts in signal activity should occur after other periods of inactivity. The most common interruption in an animal's daily routine is inclement weather. Evidence that similar peaks in territorial signaling occur after brief periods of heavy rain, which are

common in the tropics, would provide compelling support for the territorial-defense hypothesis, especially if corroborated across lizards, birds, and other chorusing taxa. Differences in territoriality across species should also result in predictable variation in the presence or absence of chorusing behavior and invite comparative analysis.

Alternatively, models predict that animals should concentrate communication during times when environmental conditions are most amenable to signal transmission (reviewed by Dusenbery [1992] and Bradbury and Vehrencamp [1998]). In birds, favorable atmospheric conditions and the absence of noise from wind (or rain) at dawn have been suggested to aid the transmission of vocalizations (Henwood and Fabrick 1979). Comparable environmental influences also affect the production of lizard visual displays (e.g., Fleishman 1992 for *Anolis* and Peters et al. 2007 for other lizards). For example, two species of Puerto Rican *Anolis* lizard increase the speed of their visual displays to compensate for increases in visual background "noise" from the movement of windblown vegetation (Ord

et al. 2007). Displaying at dawn would potentially circumvent the masking effect of background movement if wind were at its lowest in the morning. Although this did not seem to be the case in the Puerto Rican habitats so far examined (Ord et al. 2007), it remains to be tested more widely. Lizards might instead produce longer bouts of display at dawn and dusk to compensate for poor lighting. Doing so would enhance signal detection by neighbors and other adult conspecifics under conditions of poor visibility. Ambient light does vary by time of day (figs. 1, 2), but it did not explain changes in display production within species. Closer examination of interspecific differences in these environmental variables and temperature might instead reveal why diel patterns in different display types vary across *Anolis* species.

Other aspects of the behavioral ecology of chorusing species, irrespective of signal modality, also deserve further consideration. Active foragers may offset the cost associated with diverting time away from foraging by concentrating other activities, such as territorial signaling, to times when prey are less abundant. If foraging is more profitable in the middle of the day, this could lead to dawn and dusk peaks in signaling within species. Likewise, similar patterns might occur if predation pressure is lower at these times. Although anoles are generally considered sit-and-wait insectivores, variation does exist across species in time spent moving about looking for prey (Perry 1999), and prey abundance does vary between habitats (e.g., Janzen and Schoener 1968; Bullock et al. 1993). A comparison of diet and foraging modes across lizards, birds, and other chorusing species would be informative.

One important distinction exists between chorusing behavior in anoles and acoustically communicating species. Dawn choruses in bird song typically occur as a dramatic burst in production over a period of less than an hour (Staicer et al. 1996; Amrhein et al. 2004; Burt and Vehrencamp 2005; Liu and Kroodsma 2007). In contrast, fluctuations in anole signal activity are generally more gradual. Comparative study across taxa varying in signal modality, territoriality, habitat, and other ecological variables are needed to determine the potential significance of this temporal variation and, more generally, will prove critical for identifying the functional origins of chorusing behavior.

To my knowledge, this study is the first investigation of dawn/dusk "choruses" outside the acoustic modality. Many animals use signals to defend territories (Bradbury and Vehrencamp 1998), and the range of taxa that communicate acoustically and reported to perform dawn or dusk choruses is equally diverse (see references in Staicer et al. 1996). This study now extends the paradigm of dawn and dusk peaks in signal production to visual displays in lizards. It seems likely that similar diel patterns should

occur in other territorial animals using visual displays or other dynamic signals (e.g., electrical).

Acknowledgments

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