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Daily activity patterns of Whiptail Lizards (Squamata: Teiidae: *Aspidoscelis*): a proximate response to environmental conditions or an endogenous rhythm?

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Summary

1. The hypothesis that high soil temperatures are required to induce both initiation and cessation of daily activity in Whiptail Lizards (*Aspidoscelis*; formerly *Cnemidophorus*), as well as the hypotheses that hunger thresholds and high rates of evaporative water loss influence daily activity patterns, were experimentally tested in *A. inornata* and *A. gularis*.

2. Although a critical soil temperature was required to elicit the initiation of morning activity, high temperature was not a necessary stimulus for the cessation of activity.

3. Access to prey did not influence the pattern of daily activity; moreover, evaporative water loss did not appear to explain the cessation of afternoon activity.

4. Reversing the photoperiod during our experiments led only to a change in the time of initiation of daily activity (i.e. activity began 12 h later), not a significant change in the duration of daily activity.

5. These results provide strong evidence that circadian cycles can play a critical role in not only the initiation but also the *cessation* of activity.

6. While the ultimate cause (i.e. selective advantage, if any) of this unusual circadian rhythm may be related to extreme temperature, limited water supplies or some other exogenous factor, clearly, the rhythm persists in the absence of limiting environmental conditions.

Key-words: Circadian rhythm, *Cnemidophorus*, environmental constraints, reptile, temperature

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Introduction

Animal activity patterns are influenced by both exogenous and endogenous factors. While most circadian biologists would probably assume that circadian clocks drive activity patterns, it is also well known that environmental stimuli may mask endogenous rhythms by either increasing or suppressing activity (Underwood 1992). For example, stimuli such as high temperatures (Porter *et al*. 1973; Huey 1982), dehydration (Porter *et al*. 1973; Bowker 1993) and satiation (Hardy 1962; Metcalfe & Steele 2001) may suppress activity, while hunger may increase activity (Hardy 1962; Metcalfe & Steele 2001). Masking is typically defined as 'any process that distorts the original output from the internal clock whether this originates from inside or outside the body' (Minors & Waterhouse 1989, p. 30). Because of the potential for exogenous factors to mask circadian rhythms, understanding the proximate causes (i.e. exogenous or endogenous) of field activity patterns in animals can be elusive, especially under extreme conditions (e.g. desert environments). This may be particularly true in ectothermic taxa because they often exhibit a stronger physiological link to temperatures in their habitat than do endotherms.

In reptiles, temperature is known to influence physiological, behavioural and ecological characteristics, including activity patterns (Avery 1982; Huey 1982; Lillywhite 1987). Perhaps because of the strong dependence of reptiles on appropriate body temperatures for activity, most studies of field activity patterns in reptiles either explicitly or implicitly suggest that environmental temperature is the proximate determinant of both the initiation and cessation of daily activity (Pianka 1970; Porter *et al*. 1973; Huey 1982; Pianka 1984; Table 1). For instance, most diurnal lizards, including Whiptail Lizards (*Aspidoscelis* sp., formerly *Cnemidophorus* sp.), have been observed to emerge from underground retreats at particular soil temperatures, to be active for a characteristic amount of time, and to cease activity at particular (higher) soil temperatures (Pianka 1970;

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Porter *et al*. 1973; Huey 1982; Table 1). While environmental temperatures can certainly suppress activity in both ectotherms (Huey 1982; Grant & Dunham 1988, 1990) and endotherms (Bozinovic *et al*. 2000), the correlation between temperature and cessation of activity does not imply causation and does not preclude the hypothesis that the daily activity patterns observed in the field could be primarily driven by circadian clocks, which may have evolved through natural selection to avoid encountering stressful temperatures (Underwood 1992; Foa *et al*. 1994; Foa & Bertolucci 2001).

Table 1. Review of representative literature on field observations and hypothesized control of daily activity patterns in *Aspidoscelis* (formerly *Cnemidophorus*). Species names used in the table are currently recognized synonyms for names used in the cited references

Source	Species	Hypothesized control of daily activity	Beginning of morning activity	Ending of morning activity
Hardy (1962)	*A. sexlineata*	Soil temperature and hunger state	08.00–10.00 h on clear sunny days, but later if it rains	At the beginning of the hot part of the day
Kay *et al*. (1973)	*A. inornata*, *A. tigris*	Soil temperature and hunger state	First lizard seen at 08.30 when soil reached 36–38 °C	Few lizards found active after 11.00 h. One *A. inornata* observed entering burrow at 10.30 h
Medica (1967)	*A. exsanguis*, *A. inornata*, *A. tigris*, *A. neomexicana*	Soil temperature	07.00–09.00 h when soil reached 26–30 °C	13.00 h when soil reached ~50 °C
Milstead (1957)	*A. exsanguis*, *A. inornata*, *A. tigris*, *A. gularis septemvittata*, *A. tessellata*	Soil temperature	07.00–09.00 h when soil reached 28–30 °C	11.00–13.00 h when soil reached 50–52 °C.
Punzo (2001)	*A. tigris*, *A. tesselata*	Soil temperature	07.00–08.30 h when soil reached 28–30 °C	13.00 h when soil reached 50 °C
Stevens (1982)	*A. inornata*	Soil temperature	Mean soil temperature during the 1st hour of activity was 30·8 ± 1·1 °C	Mean soil temperature in final hour of activity was 47.0 ± 1.9 °C

In this study, we tested four competing hypotheses of proximate determinants of daily activity patterns in two bisexual Whiptail Lizard species, *Aspidoscelis inornata heptagramma* (Baird 1859) (Trans-Pecos Striped Whiptail; formerly *Cnemidophorus inornatus heptagrammus*, see Reeder, Cole & Dessauer 2002) and *A. gularis septemvittata* (Cope 1892) (Plateau Spotted Whiptail; formerly *C. septemvittatus*; see Reeder *et al*. 2002). We chose to use two species rather than one to test the generality of our predictions to *Aspidoscelis* as a group. Because the unusually early cessation of activity in *Aspidoscelis* has been the subject of much speculation (see above references and Table 1), and because the role of exogenous and endogenous factors in the cessation of daily activity is relatively poorly understood (Underwood 1992), we tested whether temperature, hunger, limited water availability or endogenous rhythms could account for the unusually early *cessation* of activity in these lizards. Additionally, we tested whether temperature was a sufficient masking variable that could disrupt the normal *initiation* of activity. Our prediction was that if (1) activity ceases without the influence of increasing afternoon temperatures, (2) activity ceases prior to feeding time, (3) activity ceases with water available at all times, and (4) activity ceases with routine periodicity after a predicted number of hours past the onset of the photoperiod and/or temperature cycle (hereafter referred to as photothermoperiod), even under reversed photothermoperiods, then the relatively early *cessation* of activity in *Aspidoscelis* is not the result of exogenous factors, but is primarily controlled by an endogenous rhythm.

Materials and methods

STUDY ORGANISMS

Aspidoscelis (Squamata: Teiidae) is an excellent genus for testing hypotheses of endogenous and exogenous determinant(s) of daily activity patterns because most *Aspidoscelis* in North America live in thermally harsh environments (e.g. deserts of the south-western USA), exhibit unusually brief periods of daily activity compared with other sympatric lizard genera (generally only active for 2–5 h per day; Etheridge & Wit 1993), do not defend territories (Etheridge & Wit 1993), and are known to do very well in captivity, appearing not to alter their behaviour from that in the field

(Townsend 1979). Furthermore, most *Aspidoscelis* species of the south-western USA exhibit similar thermal biology (laboratory-selected body temperatures: 39–40 °C; field active body temperatures: 38–41 °C; Milstead 1957; Hardy 1962; Medica 1967; Pianka 1970; Schall 1977; Bowker & Johnson 1980; Avery 1982; Stevens 1982) and activity patterns, even across varied habitats and geography (Milstead 1957; Medica 1967).

LIZARD COLLECTIONS, GENERAL HOUSING AND MAINTENANCE

All *A. inornata* ($n = 11$; 5 males, 6 females) and *A. gularis* ($n = 10$; 8 males, 2 females) were captured from Brewster County Texas, USA, in the Chihuahuan Desert in June 1999. Prior to experiments, all lizards were housed singly in 38-l ($50{\cdot}8 \times 25{\cdot}4 \times 30{\cdot}5$ cm^3) aquaria fitted with newspaper as a substrate and PVC tubes for refugia. Lizards were maintained in a 24 ± 3 °C room with a 12L:12D photoperiod and provided with a 75-W incandescent light as a heat source, producing a thermal gradient ranging from room temperature to >42 °C within each aquarium. Additionally, all lizards were provided with fluorescent UV lighting (Reptisun 5·0 UVB, Zoo Medical Laboratories, Inc., San Luis Obispo, CA), fed mealworms (larvae of *Tenebrio molitor*) daily (*A. inornata* received one mealworm per day and *A. gularis* received three mealworms per day; *A. gularis* is approximately three times as large as *A. inornata*), and provided a continual supply of water via a small water dish. Feeding times were altered daily to ensure that lizards would not develop food-anticipatory activity (e.g. Lague & Reebs 2000; Sanchez-Vazquez, Aranda & Madrid 2001). These husbandry conditions and experimental protocols represented seminatural conditions and at no time compromised the ethical treatment of the lizards. All experiments occurred between 4 October and 22 November 1999 to avoid any possible influences of mating season and/or reproductive behaviours on activity.

ACTIVITY CHAMBER

The activity chambers provided *Aspidoscelis* access to environmental temperatures ranging from 24 ± 0·5 °C to >50 °C both on the soil surface and below ground throughout the photophase, without any marked or significant gradual increase in average temperature throughout the day. Our temperature gradients were also spatially stable within the chambers, which differs from the thermal environment in the field where increasing temperatures can dramatically decrease or eliminate the percentage of thermally available habitat at certain times of the day in certain localities (Grant & Porter 1992). This gradient of temporally and spatially stable temperatures freed *Aspidoscelis* of environmental temperature constraints that may be imposed by either excessively high or low environmental temperatures found in the field (see above), allowing them to behaviourally thermoregulate with normal activity temperatures available both above and below ground during the photoperiod. This is important because most studies examining circadian rhythms use constant temperature regimes and/or constant darkness (determined by the experimenter), which can influence the patterns of activity observed in ectotherms. For example, some reptiles may shift from bimodal to unimodal daily activity patterns depending on the experimenter's choice of temperature regime (reviewed in Underwood 1992) and prolonged periods of constant darkness (i.e. lack of UV lighting) can be physiologically harmful to reptiles (Gehrmann 1994).

Activity chambers were created by placing eight 38-l aquaria ($50{\cdot}8 \times 25{\cdot}4 \times 30{\cdot}5$ cm^3) inside a walk-in environmental chamber set at a constant room temperature of 23·1 ± 0·2 °C. One 100-W incandescent spotlight was fixed directly against one front corner of glass on each aquarium to serve as a heat source. After the initial heating period at the beginning of the photoperiod (within 1·75 h of the onset of photophase) the temperature gradient became temporally stable. Fluorescent UV lights (Reptisun 5·0 UVB) were placed approximately 46 cm above the substrate of the aquaria; heat produced from these lights was negligible.

Each aquarium was filled to a depth of 1·9 cm with a sand substrate. To provide underground refugia, we placed five PVC pipes (26·6 cm long and 2·54 cm in diameter) in each aquarium housing *A. gularis* and six PVC pipes (23·5 cm long and 1·9 cm in diameter) in each aquarium housing *A. inornata*. All PVC pipes were partially buried in the sand with the openings exposed and placed in a standardized fashion to ensure an even distribution of underground temperatures among all aquaria. Seven aquaria were used to house lizards during the activity trials. The eighth aquarium was used to continually monitor (via a thermocouple array and data logger) the environmental temperatures available to lizards during the trials (temperatures among the seven 'lizard' aquaria were spatially and temporally equal to the temperatures within the eighth 'reference' aquarium).

ACTIVITY TRIALS

Two photoperiod regimes, normal and reversed, were used during our observations to examine the influence of photoperiod on daily activity patterns. Because we could test only seven lizards at once, the 21 lizards (11 *A. inornata* and 10 *A. gularis*) were divided into three blocks. Each block, and thus every lizard, was subjected to all trials (see below) in both photoperiod regimes.

Initiation time of observations varied among trials (see below). However, once initiated, one observation per lizard (to avoid pseudoreplication; Hurlbert 1984) was made every 2 h until the end of the trial. During each observation, the observer entered the environmental chamber and quickly recorded the position of each lizard; lizards were scored as ‘active’ if they were on the surface and ‘inactive’ if they were in a burrow (Etheridge & Wit 1993).

In addition to the bi-hourly observations, a video-camcorder was stationed in front of randomly chosen aquaria to allow us to make complete daily behavioural observations without influencing the lizards. This was done to ensure that our bi-hourly spot-checks were not biased, as well as to gather additional information on times of feeding and drinking. Four individuals of each species were monitored with the camcorder.

To reduce the possibility of dehydration influencing the results, and therefore to indirectly test Bowker’s (1993) hypothesis that high rates of evaporative water loss associated with high body temperatures may be a proximate limiting factor resulting in reduced daily activity in *Aspidoscelis*, water was continually available to all lizards throughout the trials.

Normal photoperiod

Prior to trials, all lizards were allowed 3 days to acclimate to the environmental chambers under a ‘normal’ 12L:12D photoperiod regime (lights on at 08.00 h, lights off at 20.00 h). Three feeding regimes were used to evaluate the effects of feeding on activity. Further, to test whether our repeated daily observations affected the activity of the lizards, we varied the time we began the observations. From these protocols we generated the following five trials: (A) fed and began checking activity at 08.00 h ; (B) fed at 14.00 h and began checking activity at 08.00 h ; (C) *not* fed and began checking activity at 08.00 h ; (D) fed at 08.00 h and began checking activity at 14.00 h ; and, lastly (E) fed at 08.00 h and began checking activity at 16.00 h. The order of trials was randomly assigned among each of the three blocks to reduce the chance of systematic carryover effects. In all trials (except for the trial category ‘not fed’), lizards were fed large meals to ensure satiation: *A. gularis* were fed ten mealworms per day and *A. inornata* were fed three mealworms per day; any mealworms not eaten by the end of the trial (20.00 h) were removed at that time.

Reversed photoperiod

All lizards were allowed a minimum of 7 days to acclimate to the reversed photoperiod (12L:12D; lights on at 20.00 hours, lights off at 08.00 hours). The protocols of our observations were similar to those used in the normal photoperiod trials, save for two differences: (1) observation times of all trials were shifted by 12 h so that they would be diurnally comparable to those under the normal photoperiod regime, and (2) an additional trial was added to test whether or not a critical temperature was required for the initiation of morning activity. The additional trial was similar to the reversed photoperiod trial A (fed at 20.00 hours/obs at 20.00 h), but lacked a significant heat source; although the fluorescent lights came on at 20.00 hours, the incandescent spotlight did not.

STATISTICAL METHODS

Decreased afternoon activity could be an artefact of a human observer scaring lizards underground during successive observation periods. To test this, the frequency of surface-active lizards (within species) at each observation in trial A (fed at 08.00 hours/obs at 08.00 h) was compared with the frequency of surface-active lizards at corresponding observations in trials D (fed at 08.00 h /obs at 14.00 h) and E (fed at 08.00 h /obs at 16.00 h) using the two-tailed ‘exact’ binomial test for the McNemar test for the significance of changes, when the total number of changes is fewer than 25 (Sokal & Rohlf 1995). The McNemar test is used for repeated measures designs (i.e. repeated testing of the same individuals) when the dependent variable is a frequency (in this case, the number of lizards on the surface at each observation period). If patterns of surface activity were purely a result of repeated disturbance by the human observer, then lizards in trials D and E should have been active in the afternoon, whereas those in trial A should not. The McNemar test also was used to compare surface activity in the trials with normal photoperiod to those with reversed photoperiod. Equations from Sokal & Rohlf (1995) were used to calculate the probability levels.

To test if the feeding regime affected lizard activity, each bi-hourly observation period in trials A (fed at 08.00 h/obs at 08.00 h), B (fed at 14.00 h/obs at 08.00 h), and C (did not feed/obs at 08.00 h) was compared using Cochran’s *Q*-test, a repeated-measures test for frequency data when the number of treatments ≥ 3. The chi-square goodness of fit test was used to test the null hypothesis of no difference in activity among sexes prior to analyses; because there was no significant difference in activity among sexes ($\chi^2 = 16{\cdot}83$; d.f. = 14; $P = 0{\cdot}27$), sex was excluded from all of the above analyses. The Cochran’s *Q*-test and chi-square test were performed using the STATISTICA software package (Windows ver. 5·1, StatSoft, Inc. Tulsa, OK).

Results

In the trials with normal photoperiod (lights on 08.00 h, off 20.00 h) both species exhibited similar patterns of activity, with activity concentrated in the late morning, decreasing markedly by 12.00 h, and ceasing by *c*. 14.00 h (Fig. 1).

No significant differences in percentage of active lizards were detected between trials A (fed at 08.00 h/obs at 08.00 h) and D (fed at 08.00 h/obs at 14.00 h) or A and E (fed at 08.00 h/obs at 16.00 h) for either species ($P > 0{\cdot}5$ in all comparisons; *A. inornatus*, $n = 11$; *A. gularis*, $n = 10$), indicating that the presence of the observer was not the stimulus that caused the lizards to retreat underground. No significant differences were

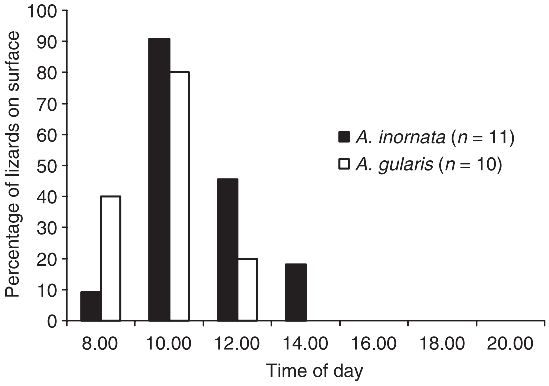

Fig. 1. Surface activity of *Aspidoscelis inornata* and *A. gularis* in laboratory activity chambers during trial A (fed and began observations at 08.00 h). Both species exhibited similar patterns of surface activity, with activity ceasing in the early afternoon, despite temporally stable chamber temperatures and a continual supply of drinking water.

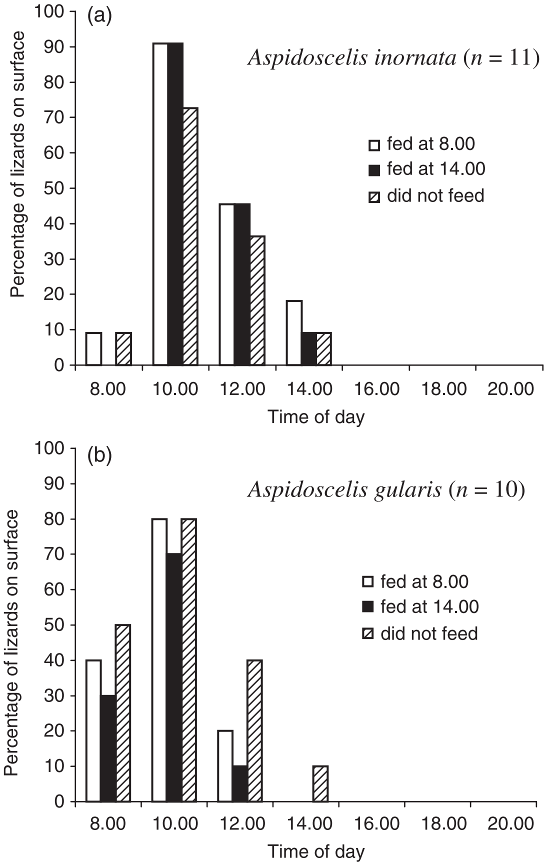

Fig. 2. Surface activity during trials A (fed at 08.00 h), B (fed at 14.00 h) and C (did not feed). If lizards retreated underground after becoming satiated, less afternoon activity should be exhibited in trial A than in trials B and C. No significant differences were detected for either species during any observation period ($Q_2 < 4{\cdot}7$, $P > 0{\cdot}09$ in all comparisons): (a) *Aspidoscelis inornata*; (b) *A. gularis*.

detected among trials A (fed at 08.00 h/obs at 08.00 h), B (fed at 14.00 h/obs at 08.00 h) and C (*not* fed/obs at 08.00 h) in either species ($Q_2 < 4{\cdot}7$, $P > 0{\cdot}09$ in all comparisons; *A. inornatus*, $n = 11$; *A. gularis*, $n = 10$; Fig. 2), indicating that lizards did not retreat underground after becoming satiated, or remain above ground beyond the usual retreat time when food was withheld.

Although there was a non-significant trend for decreased activity during the trials with reversed photoperiod ($P \geq 0{\cdot}25$ in all comparisons for both species; *A. inornatus*, $n = 11$; *A. gularis*, $n = 10$; see Fig. 3), the pattern of activity was similar in both reversed and normal photoperiod trials: most activity occurred in the first few hours of the photophase and activity ceased by approximately 6 h into the photophase, as would be predicted if cessation of activity is driven by an endogenous rhythm entrained to the photothermoperiod. Although lizards were given at least 7 days to acclimate to the reversed photoperiod before trials began, we noticed that most lizards appeared to have acclimated to the reversed photoperiod (i.e. reversed their activity cycle) within the first 2 days.

During the trials with fluorescent lights only (i.e. no spotlight), the chamber temperatures were a near-constant 23·1 ± 0·2 °C both above and below ground. No *A. inornata* were observed on the surface during these trials. Four of 10 *A. gularis* were on the surface at 08.00 h; one additional individual (not one of the previous four) was on the surface at 10.00 h, but none were on the surface during subsequent observations.

Our results and conclusions do not change (in fact the *P*-values generally increase as we would expect) when the two species are treated as a single statistical population in the analyses (i.e. analysed at the genus level to increase sample sizes to 21) or when the probabilities from independent tests of significance (i.e. each species computed separately, as presented above) are combined using meta-analysis techniques following equations in Sokal & Rohlf (1995), suggesting that our non-significant results are not due to insufficient power, but rather are a true feature of the biology of *Aspidoscelis*.

Discussion

Field activity studies of diurnal desert lizards, including *Aspidoscelis*, have noted that both initiation and cessation of daily activity patterns generally correlate with particular soil temperatures. Specifically, initiation of daily activity has been hypothesized to be dependent upon the achievement of some critical soil temperature for lizard emergence, while cessation of activity is hypothesized to be the direct result of increasing afternoon soil temperatures that may be thermally stressful.

To test the hypothesis that increasing afternoon temperature is *required* to cause the unusually early cessation of activity in *Aspidoscelis* we made behavioural observations of lizards provided with a temporally stable thermal gradient, both above and below ground, with no increase in average temperature occurring after *c.* 09.45 hours. Under these conditions

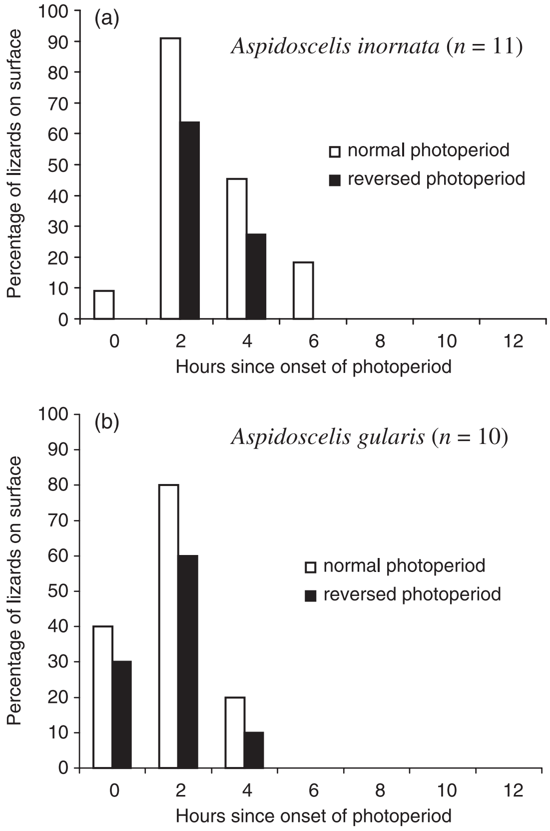

Fig. 3. Surface activity during trial A under a normal photoperiod regime (lights on at 08.00 h) and a reversed photoperiod regime (lights on at 20.00 h). Similar activity patterns were exhibited under both photoperiod regimes ($P \geq 0{\cdot}25$ in all comparisons for both species): (a) *Aspidoscelis inornata*; (b) *A. gularis*.

temperature is not activity limiting and there is no external thermal cue that might cause the lizards to retreat in anticipation of thermally stressful temperatures. Despite the lack of increasing afternoon temperatures, we observed similar patterns of daily activity in *A. inornata* and *A. gularis*, with activity concentrated in the morning, reduced dramatically by noon, and ceasing by *c.* 14.00 h, a pattern that is strikingly similar to previously published field (Table 1) and laboratory (Townsend 1979) observations of *Aspidoscelis*. Since activity patterns appear similar to those in the field, and cessation of activity occurs with predictable periodicity (e.g. 2–6 h after onset of photothermoperiod), we can conclude that increasing afternoon temperature is *not required* to cause the unusually early cessation of activity in *Aspidoscelis*. Thus, while we acknowledge that high environmental temperatures and a corresponding reduction in thermally suitable habitat patches may constrain activity times in some lizards (Huey 1982; Grant & Dunham 1988, 1990; Grant & Porter 1992), we note that this does not appear to be a necessary proximate cause of afternoon retreats in *Aspidoscelis*, at least in the two species we studied.

Desert environments may also limit activity of ectotherms at high temperatures because rates of evaporative water loss (EWL) increase with both temperature and activity (Porter *et al.* 1973; Bowker 1993). Because water lost must be replaced through water-rich food sources, metabolic water production or drinking, reduced daily activity patterns are hypothesized to be advantageous in extreme thermal environments where these replenishing factors are limited (Porter *et al.* 1973; Bowker 1993). Although we did not directly measure or alter evaporative water loss (EWL) during our trials, we provided *Aspidoscelis* with a continual source of drinking water. Data from the video-camcorder confirmed that the lizards readily drank from this water source. If high rates of EWL and concomitant dehydration were the proximate cue that drives these desert lizards underground (Bowker 1993), then it seems likely that when water is not limiting, the lizards would simply remain active throughout the day, drinking as necessary. However, our results suggested otherwise: the lizards retreated underground early in the day, despite the presence of a continual water supply. We suggest that EWL cannot be considered the proximate cause of the retreating behaviour and relatively brief daily activity patterns in *Aspidoscelis*. Further tests of this hypothesis could include (1) the manipulation of ambient humidity levels to determine if increased humidity, and thus lower EWL rates, leads to increased surface activity and (2) manipulation of access to water supplies. Similarly, because the presence or absence of biotic factors (e.g. potential mates) could influence the desire of lizards to remain active longer under favourable conditions, these manipulations could be completed during the breeding season and/or in the presence or absence of potential mates.

In contrast to Hardy's (1962) hypothesis that successful foraging is followed by early retreat times in *Aspidoscelis*, we observed similar patterns of activity during trials where lizards were fed early (trial A – fed at 08.00 h), late (trial B – fed at 14.00 h) and not at all (trial C – not fed). If Hardy's hypothesis explained activity in our lizards, we would have observed lizards fed early (trial A) retreating underground earlier than those fed later (trial B) or those that were not fed (trial C), with unfed lizards exhibiting the longest duration of daily activity. This pattern clearly was not evident in either *A. inornata* or *A. gularis*. It is unlikely that these results are an artefact of our experimental protocols. During the trials where food was offered, an overabundance of food was given to ensure satiation, and the food was placed in a small dish from which the lizards regularly ate. Data collected from the video-camcorder confirmed that both species did indeed eat during the morning hours after the 08.00 h feedings; however, both species rarely ate during trials where they were fed late (trial B – fed at 14.00 h), since most lizards had retreated underground by the time of the 14.00 h feeding. Thus, the similar pattern of activity we observed during trials A, B and C was not the result of lizards not feeding or achieving satiation during trials.

Our results suggest that cessation of activity in *Aspidoscelis* must be either an innate or acquired behaviour that operates even in the absence of most limiting environmental variables, such as extreme high temperatures, water availability or food availability. Therefore, we hypothesize that activity cycles in *Aspidoscelis* follow a circadian clock, which is entrained to (i.e. assumes the period of) the photothermoperiod. To further test our hypothesis, we subjected the same lizards to a reversed photothermoperiod, with the expectation that this laboratory manipulation would cause a matching reversal in timing of activity patterns. This prediction was correct: after a short (2–7 day) acclimation period the lizards had fully reversed their activity, with cessation of activity occurring 2–4 h after the start of the new onset of photothermoperiod, as would be predicted under the hypothesis of a circadian clock entrained to the exogenous photothermoperiod (Underwood 1992). Further tests could include manipulations of photophase duration to determine if *Aspidoscelis* change the duration of their daily activity correspondingly or if they exhibit a fixed duration of activity regardless of photoperiod. Nevertheless, we consider the observed pattern of activity of *Aspidoscelis* to be consistent with the hypothesis of control by a circadian clock, regardless of whether or not the period of daily activity would vary with variations in photophase duration (e.g. seasonally) (see definition of circadian rhythm in Underwood 1992, p. 231), so long as the cycle repeated itself every solar day (under a given photoperiod regime).

Our results support the hypothesis that particular soil temperatures are required for the initiation of daily activity. Suboptimal temperatures (i.e. during the fluorescent lights-only trials) resulted in little activity, other than a few *A. gularis* that were briefly surface active at the initiation of the photophase, as if in anticipation of an environmental warming that never occurred. Thus it appears that, at least in some *A. gularis*, there may be a circadian clock controlling times of emergence, which has been found to be fairly widespread among lizards (Underwood 1992), but that the normal circadian activity cycle is probably suppressed by low temperatures, indicating that exogenous factors can mask the circadian rhythm of activity in *Aspidoscelis*. Similar masking patterns have been found in the Desert Iguana (*Dipsosaurus dorsalis*) when light was provided at anticipated emergence times in the absence of appropriate soil temperatures (Porter *et al*. 1973).

In summary, we simultaneously tested four explicit hypotheses regarding daily activity patterns in diurnal desert lizards, using *A. inornata* and *A. gularis* as our model organisms. We found that cessation of daily activity occurred with routine periodicity (1) without the influence of increasing afternoon temperatures, (2) without being influenced by feeding time, (3) without being limited by water availability, and (4) under a reversed photothermoperiod. Our results suggest that the unusually brief daily activity in *Aspidoscelis* is not primarily determined by exogenous factors, but instead follows a circadian rhythm entrained to the photoperiod and/or temperature cycle. Furthermore, we found that the circadian clock can be masked by temperature, and that an increase in soil temperature is generally required for the initiation of daily activity.

While our results are consistent with previous studies of activity cycles in other lizards, we note that, to our knowledge, this is the first study to examine circadian rhythms in the family Teiidae (see Underwood 1992), and to primarily focus on determining if the *cessation* of activity is under endogenous control (reviewed in Underwood 1992) while testing ectotherms in a seminatural environment (i.e. where animals choose body temperatures and UV lighting is available during the photoperiod). Our study complements the more traditional studies that use constant temperature and/or darkness regimes (Underwood 1992; Foa *et al*. 1994; Bertolucci *et al.* 1999; Foa & Bertolucci 2001), and provides strong evidence that circadian cycles can play a critical role in not only the initiation but also the *cessation* of activity. While the ultimate cause (i.e. selective advantage, if any) of the unusual circadian rhythm in *Aspidoscelis* may be related to extreme temperature, limited water supplies or some other exogenous factor, clearly, the rhythm persists in the absence of limiting environmental conditions.

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