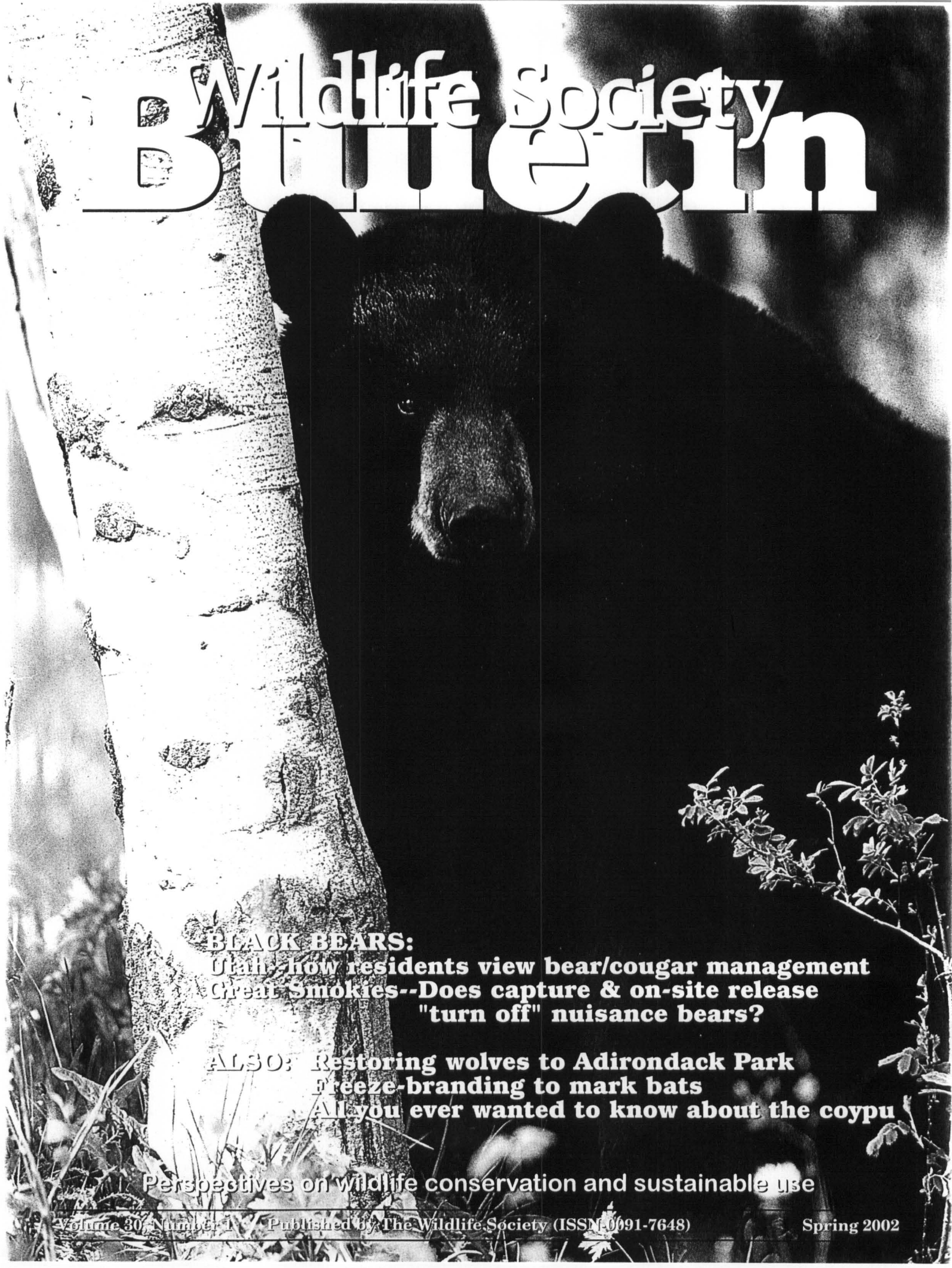

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Black bear in open aspen forest.
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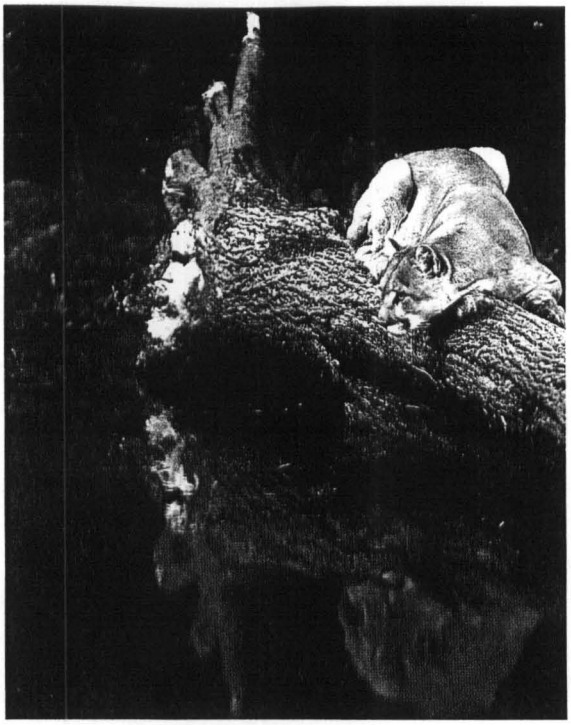

Cougar and reflection, page 2 Photo by Carlyn Iverson/Absolute Images

TABLE OF CONTENTS

Human Dimensions

Utah stakeholders' attitudes toward selected cougar and black bear management practices
Tara L. Teel, Richard S. Krannich, and Robert H. Schmidt 2

New Yorkers' attitudes toward restoring wolves to the Adirondack Park
Jody W. Enck and Tommy L. Brown 16

Traditional Knowledge

Use of traditional knowledge by Rakiura Maori to guide sooty shearwater harvests
Philip O'B. Lyver 29

Population Modeling

An online wild turkey population dynamics model
Elizabeth N. Brooks, Russell Alpizar-Jara, Kenneth H. Pollock, David E. Steffen, James C. Pack, and Gary W. Norman 41

Survey Methods

Review of big-game survey methods used by wildlife agencies of the western United States
Michael J. Rabe, Steven S. Rosenstock, and James C. deVos, Jr. 46

Using distance sampling to estimate seasonal densities of desert mule deer in a semidesert grassland
Kiana K. G. Koenen, Stephen DeStefano, and Paul R. Krausman 53

Population Indices

Comparison of indices to estimate abundance of dusky-footed woodrats
Keith A. Hamm, Lowell V. Diller, and David W. Kitchen 64

Leaf litter bags as an index to populations of northern two-lined salamanders (*Eurycea bislineata*)
Rebecca J. Chalmers and Sam Droege 71

Nongame Avifauna

Temperature effects on Florida applesnail activity: implications for snail kite foraging success and distribution
Amanda J. Stevens, Zachariah C. Welch, Philip C. Darby, and H. Franklin Percival 75

Temperature effects on Florida applesnail activity: implications for snail kite foraging success and distribution

Amanda J. Stevens, Zachariah C. Welch, Philip C. Darby, and H. Franklin Percival

Abstract The endangered Florida snail kite (*Rostrhamus sociabilis*) feeds exclusively on applesnails (*Pomacea paludosa*), yet we lack direct observations that link applesnail behavior to snail kite foraging success. The purpose of our study was to evaluate the temperature-activity profile of applesnails in the context of restricted foraging opportunities for snail kites. Applesnail activity was monitored in water temperatures ranging from 2–24°C. We found no active snails in water <13°C. Evaluation of a suite of candidate models indicated that temperature changes, observation period, study tank, and some interactions contributed to an explanation of the trends in the activity data, but temperature had the most prominent effect. Burial was a common response (92% of snails) to temperatures <10°C. Buried snails and snails rendered inactive by cold temperatures are not accessible to kites. Our data help explain the range restriction of snail kites to central and southern Florida despite the presence of applesnails in north Florida and may explain seasonal shifts in kite distribution and the peak in nest initiation by snail kites. Given the temporal constraint imparted by passing cold fronts on the initiation of snail kite nesting activity, water managers concerned with snail kite nesting success need to consider timing of water withdrawals such that suitable conditions exist long enough to permit successful completion of their breeding cycle.

Key words activity, applesnail, *Pomacea paludosa*, prey availability, *Rostrhamus sociabilis*, temperature, snail kite

The Florida applesnail (*Pomacea paludosa*; common name from Turgeon et al. 1998) is the nearly exclusive food source for the Florida snail kite (*Rostrhamus sociabilis*; Snyder and Snyder 1969, Sykes et al. 1995). Despite the importance of applesnails in the life history of this endangered raptor, no one has studied the foraging success of the snail kite relative to snail abundance or behavior. This is due in large part to the difficulty in collecting and observing snails in their natural environment (Darby et al. 1999). In this paper we report observations on temperature-related changes in snail behavior that likely affect foraging success and distribution of the snail kite.

Foraging success for predators depends on prey abundance and availability (i.e., detectable and accessible prey items). Snail kites forage by visually

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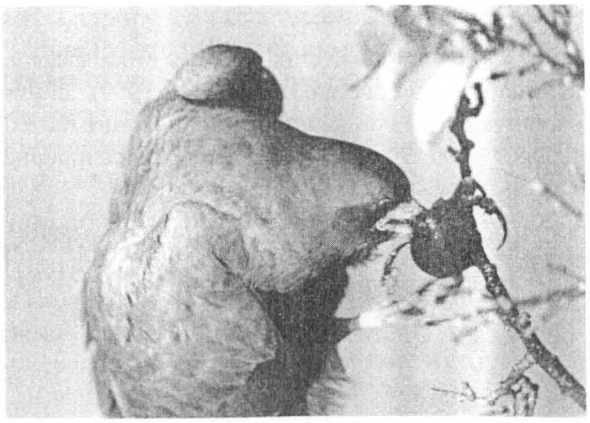
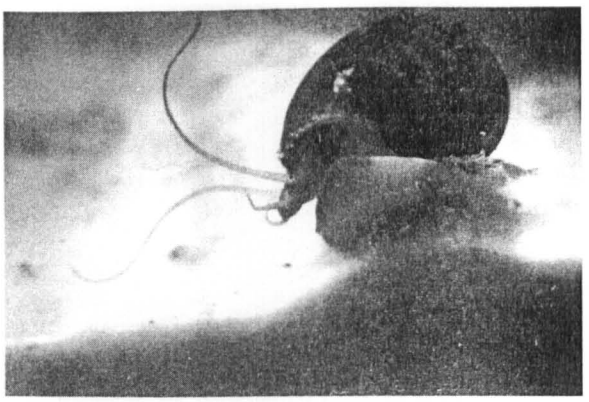
surveying the water for applesnails (Sykes et al. 1995). The Florida applesnail belongs to a family of snails (Ampullariidae) common to subtropical and tropical wetlands throughout Central and South America, Africa, and India. Although quite large (the >100 species range from approximately 30 to 150 mm in diameter), they are generally cryptic in color and can be difficult to find in vegetated habitats (Darby et al. 1999). Snail kites most likely capture snails that extend a siphon to the surface to breathe air (Bennetts et al. 1994), although exactly how kites detect their prey is unknown. For example, we do not know whether kites detect snails that dimple the water's surface with their siphon, whether kites detect the pumping action during inspiration (McClary 1964), or whether kites can simply see a stationary or moving snail amidst the background of wetland macrophytes, periphyton, and substrata. Given that snail kites do not plunge into the water to capture snails, and knowing their leg length, we do know that snail captures by kites are limited to the top 16 cm of the water column (Sykes et al. 1995). Successful foraging by kites requires standing water; dry-downs induce kites to move to flooded habitats (Takekawa and Beissenger 1983).

Snail activity and rates of surface inspiration decrease with decreases in temperature (McClary 1964), which should reduce foraging success of snail kites. We expect colder temperatures to suppress activity for any gastropod, but temperature-activity profiles differ even between species in the same region (Cameron 1970). Limited information is available on specific temperature-activity relationships of Florida applesnails. McClary (1964) observed a 2.7-fold increase in number of snail surface inspirations as temperatures increased from 12°C to 26°C, and snails spent 1.5 times longer at the surface in the warmer temperature. McClary (1964) did not describe general snail activity (e.g., movements, burial) below 16° C, and unfortunately, there is some question regarding the correct identification of the species (Turner et al. 2001). Applesnails and snail kites inhabit areas in central Florida where average monthly temperatures in winter fall below 16°C (Chen and Gerber 1990). Daytime temperatures <15°C occur frequently (33% of years), even in the Everglades of south Florida (Frederick and Loftus 1993). Information on cold temperatures and snails is therefore ecologically relevant, especially considering other snail predators whose ranges extend north of the snail kite (e.g., reptiles and other birds, see Darby et al. 1999). Cary (1985) described declining snail kite foraging success at colder temperatures, but made no direct observations on snails. Hanning (1979:74) stated that snails respond behaviorally to "cold winter temperatures" by burrowing into the substrate, but provided no information on specific temperatures or how he derived this conclusion. The purpose of our study was to determine the proportion of snails rendered inactive by dropping temperatures, to confirm whether burial is a common response to cold temperatures by applesnails, and to relate our findings to snail kite distribution and foraging success.



Snail kite (a male) eating an applesnail. Photo by Rob Bennetts.



Florida applesnail from the Upper St. Johns Marsh. Photo by Phil Darby.

Methods

The adult snails (shell widths 30.9 mm±4.4 mm) that we observed were part of an experiment on water manipulations and were already distributed in tanks before we began our observations on activity. Snails were collected from the Upper St. Johns Marsh, Indian River County, Florida, from 15 February

through 5 March 1998. We observed 86 snails (20–23/tank) in 4 285-L polyethylene tanks (120 × 61 × 46 cm), each with a 13-cm-deep sand substrate. The tanks were housed under a plastic tarp outside the Florida Caribbean Science Center (U.S. Geological Survey, Gainesville, Florida). We placed plastic netting (6-mm mesh) over tanks to prevent snails from escaping. Water levels in the tanks were maintained at 15 cm above the substrate. Tanks were cleaned every 7–10 days with a siphon, and the water was replaced with fresh well water (consistently 21°C). Snails were fed lettuce, spinach, and bladderwort (*Utricularia* sp.) in sufficient supply to exceed demand.

We monitored snail activity during 3 observation periods between 12 March and 29 April 1998 (hereafter the spring study), during which passing cold fronts resulted in water temperatures changing from >20°C to <14°C. Dates for each observation period were 12–18 March (observation period 1), 10–19 April (observation period 2), and 24–29 April (observation period 3). Tanks were subject to ambient temperature. The water was not changed during the observation periods to avoid artificially raising the temperature. We recorded numbers of live snails and active snails every 1–2 days during each observation period. We defined an active snail as one moving, or with extension of the tentacles and body. We took water temperature and activity data between 1300 and 1500 EST.

We evaluated the relationship between snail activity and water temperature using spring study data. We recorded temperature, number of active snails, and total live snails on each observation day. We calculated proportion of active snails in each tank on a given observation day as total active snails/total live snails. We observed snails for 6, 7, and 5 days for observation periods 1, 2, and 3, respectively. We collected 72 activity data points ($n=24$, $n=28$, and $n=20$ for observation periods 1, 2, and 3, respectively) among the 4 tanks. We considered 3 independent variables (temperature, observation period, and tank) and their interactions during model selection for the statistical analysis. We considered tank and observation period as class variables with a separate parameter for each tank or observation period. However, because temperature is continuous, we estimated a slope and intercept parameter, rather than a separate parameter for each specific temperature. We compared Akaike's information criteria (AIC) values derived from the equation $AIC = -2\ln(\mathcal{L}) + 2k$ (Burnham and Anderson 1998). We obtained values of $\ln(\mathcal{L})$, the log likelihood ratio statistic, for each model considered from PROC GENMOD in the SAS statistical package (SAS Institute, Inc. 1989). The second term, $2k$, represents number of parameters estimated in the model (k) multiplied by 2. We evaluated a suite of candidate models that included each main effect separately, as well as all possible combinations of 2-way and 3-way interactions. The most parsimonious model selected, based on the minimum AIC value (Burnham and Anderson 1998), included temperature, observation period, and tank effects with one 2-way and the 3-way interactions (Table 1). We report the type III likelihood ratio statistics from the logistic regression for each of the effects in the selected model.

During the spring study we noticed burial was common, but we did not record observations on buried snails. We therefore made additional notes on snail response to temperatures <10°C during strong cold fronts from 26–31 December 1998 and 4–5 January 1999 (hereafter the winter study). Snail positions were described as buried (no shell visible, snails found by probing the substrate),

Table 1. Candidate models for the Florida applesnail temperature–activity data and their corresponding number of parameters (np), AIC scores, and the difference in AIC between each model and the selected model with the least AIC.

Model Effect(s)[a]	np	AIC	ΔAIC
TEMP, OP, TANK, TEMP*OP, TEMP*OP*TANK[b]	15	1,331.51[c]	0.00
TEMP, OP, TANK, TEMP*OP	9	1,332.73	1.21
TEMP, OP, TANK, TEMP*TANK, TEMP*OP*TANK	16	1,333.51	2.00
TEMP, OP, TANK	7	1,334.23	2.72
TEMP, OP, TANK, OP*TANK, TEMP*OP*TANK	19	1,335.52	4.01
TEMP, OP	4	1,343.76	12.25
Fully saturated model (all possible interactions)	24	1,345.52	14.01
TEMP	2	1,353.07	21.56
OP	3	1,498.54	167.03
TANK	4	1,529.51	198.00

[a] A suite of models with all possible combinations of main effects and their interactions were evaluated. Not all models are shown; however, the table includes all models with ΔAIC < 4.

[b] Abbreviations: TEMP = temperature, OP = observation period.

[c] The least AIC value indicates the most parsimonious model for the logistic regression.

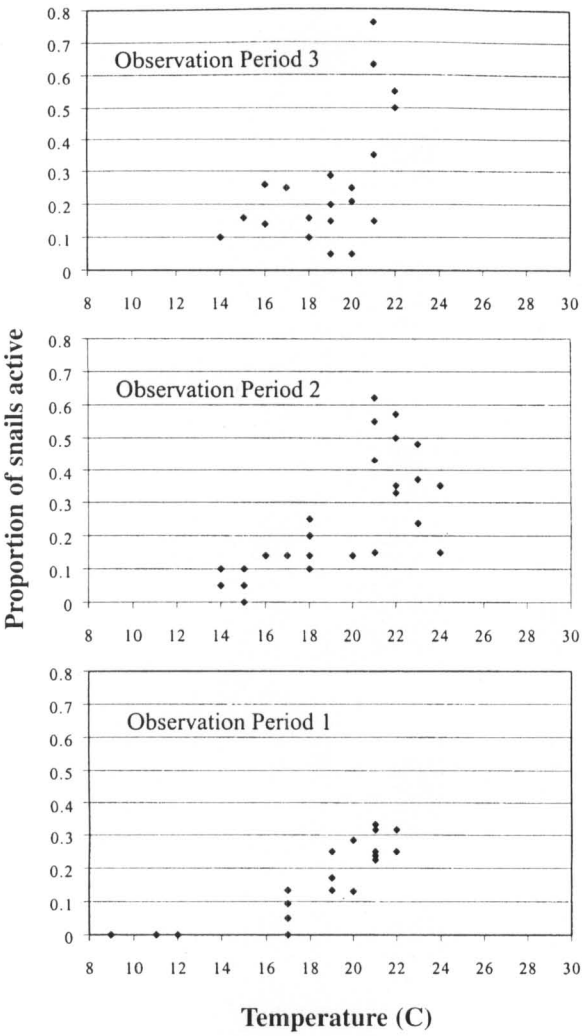


Figure 1. Proportion of active Florida applesnails as a function of temperature, spring 1998. Data points represent a single tank at a given temperature, except that 4 tanks at 9°C and 3 tanks at 12°C in observation period 1 had 0 active snails.

partially buried, or not buried within the sand substrate. We marked snail positions with colored toothpicks in case they moved, although none did. Tanks from the winter study each contained 9-15 adult applesnails (shell widths 28.9 mm±3.3 mm).

Results

In the spring study, tank temperatures ranged from 9-22°C in observation period 1, 14-24°C in observation period 2, and 14-22°C in observation period 3; the proportion of active snails ranged from 0-0.76 (Figure 1). We found no active snails (out of 86 total) in water temperatures <13°C. As commonly observed using AIC (Spendelow et al. 1995), the selected model also included terms that would not be considered significant at $\alpha = 0.05$ using likelihood ratio tests (Table 2). Impending deaths contributed little, if any, to the spring activity data, as only 4 out of the original 86 snails died during the study period (2 in March, 2 in April) and only 1 died in the 2 weeks following termination of the study.

Table 2. Likelihood ratio statistics for the selected model of Florida applesnail temperature–activity data.

Model Effect(s)[a]	df	χ^2	$P > \chi^2$
TEMP	1	141.16	≤0.001
OP	2	4.94	0.0846
TANK	3	3.16	0.3677
TEMP*OP	2	4.55	0.1027
TEMP*OP*TANK	9	13.21	0.1532

[a] Abbreviations: TEMP = temperature and OP = observation period.

Water temperatures in the winter study ranged from 2-9.5°C. No snails were active during this time; 26±8% (mean±SE) were completely buried, 66±1% were partially buried, and 8±4% were resting on top of the substrate. Two of the 3 snails on the substrate surface died. None of the buried or partially buried snails died during the winter observation period. At temperatures <8.0°C, all visible snails (partially buried or not buried) were withdrawn completely into their shells. At this point, water circulation likely ceased, as no openings could be seen between their opercula and aperture. As temperatures rose from 9 to >10°C, snails remained in their resting positions, but all visible snails had their opercula extended beyond their shell, presumably circulating water. No further observations were recorded as temperatures increased.

Discussion

The model selection procedure and associated likelihood ratio statistics indicated clearly that changes in applesnail activity were predominantly the result of a change in water temperature. For the selected model, there was 73.7% concordance (see SAS 1992) between the predicted and observed activity levels. It should be noted, however, that Burnham and Anderson (1998) suggested that any model with $\Delta AIC < 4$ may be considered a reasonable model for explaining trends in the data. All the

models of snail activity with ΔAIC<4 included temperature as a separate affect, and most interaction terms included temperature (Table 1). Tank, observation period, and associated interaction terms in these models may reflect the constraints of the study design. Because we depended on ambient temperature changes for the temperature effect, the 3 observation periods were completed in a nonconsecutive time series spanning nearly 7 weeks. As a result there was a different range of temperatures for each observation period, and there may have been other associated time affects (see below). Tank position resulted in differential exposure to sunlight that resulted in temperature differences of 1 to 3°C between tanks for any given day. This tank effect changed across observation periods due to the shift in sun position over 7 weeks.

The water temperatures recorded in our outdoor tank study were similar to those in the applesnail's natural habitats in central Florida. During field sampling of applesnails in central Florida (wetlands in Osceola and Indian River counties), we have measured midday water temperatures from 11°C (in February) to 38°C (in May; P. C. Darby, unpublished data).

When inactive and partially or completely buried in <13°C water, snails would not be available to kites. Our data were consistent with observations by Cary (1985), who noted that capture rates of snails by kites dropped to zero at water temperatures <10°C. Capture rates then increased nearly linearly from 11°C up to 30°C, likely resulting from greater visibility of the snails due to increased snail movement and associated inspiration at the surface of the water. In our study, the greatest incremental increases in snail activity occurred in water >20°C (Figure 1; observation periods 2 and 3).

Burial in response to dropping temperatures has been reported for other aquatic snails (Boerger 1975). Observations of temperature and invertebrate behavior have not been directly linked to predators inhabiting Florida's subtropical wetlands, but Frederick and Loftus (1993) described a similar temperature-behavior pattern for fish preyed on by wading birds in the Everglades. In their laboratory observations, inactivity and burial by fish occurred between 5°C and 9°C. As pointed out by Frederick and Loftus (1993), acclimation history may be important in the precise temperature-activity profile. Acclimatization has been shown to affect cold temperature tolerance in gastropods (McMahon 1983) and may have contributed to the inclusion of the observation period effect noted in the discussion of model selection. Activity generally increased from observation period 1 to 3 (Figure 1). However, other factors, such as increased activity associated with the snail's reproductive season (Odum 1957; Hanning 1979; P. C. Darby, unpublished data), may have been influential across observation periods. Another issue affecting our data interpretation was that a significant proportion of the study population, typically >50%, remained inactive at temperatures >20°C. Longer time periods of observation may be appropriate to reduce the probability of encountering "resting" snails. McClary (1964) also observed a significant proportion (>30%) of inactive *Pomacea* snails held in 26°C water with periods of inactivity ranging from 5–170 minutes in duration.

Although applesnails commonly occur north of Orlando, Florida, snail kites do not (Sykes et al. 1995). Restriction of kite range to central and southern Florida may be explained by suppressed snail activity during the 3–4 months when mean monthly temperatures are <15°C north of Orlando (Chen and Gerber 1990). Seasonal movements by kites from north to south within their range (Sykes et al. 1995) could be explained by colder temperatures and associated suppressed snail activity. Historically, kites were reported north of Orlando (Sykes et al. 1995), but no information is available on seasonal latitudinal shifts in kite distribution in their former range.

Breeding attempts by kites are delayed following the passage of cold fronts in Florida (Bennetts and Kitchens 1997) and are likely related to temporary declines in applesnail availability due to inactivity and burial. Peak nest initiation for the Florida snail kite population occurs in March (Bennetts and Kitchens 1997). Average monthly temperatures in central and south Florida remain >18°C from March through November (Chen and Gerber 1990), at least 4°C above the point when at least some snails were found active in our study. Kite nesting may, in part, be timed to avoid suppressed snail availability during winter.

The snail kite reproductive season has been described as a shifting window of opportunity constrained by fluctuating environmental conditions (Bennetts and Kitchens 1997, Kitchens et al. 2001). Passing cold fronts that suppress snail activity constitute a temporal constraint (related to food availability) on the initiation of snail kite nesting. The

window of opportunity for breeding also can be constrained by water levels falling below ground level (i.e., a drying event). Drying events also render applesnails unavailable to kites (Bennetts and Kitchens 1997). Under natural hydrologic conditions, these wetland-drying events typically occur toward the terminal end of the snail kite breeding season (Bennetts and Kitchens 1997) Water control structure installation and associated water management implementation have altered the natural hydrologic regime since the 1950s (Light and Dineen 1994). The result has been earlier and more frequent drying events that can truncate the length of the snail kite breeding season over portions of their range (e.g., Everglades National Park; Beissinger 1986). Given the potential constraint of cold temperatures on the timing of the initiation of snail kite breeding, water managers concerned with snail kite nesting success need to consider timing of water withdrawals later in the kite's breeding season such that suitable conditions exist long enough to permit successful completion of their breeding cycle.

Our data also provide important information related to the field collection of applesnails as efforts continue to understand their ecology and impacts of water management on their distribution and abundance. Funnel traps have been used to collect and study applesnails in wetland habitats (Darby et al. 2001). Trapping success depends on snail movements, and collection will therefore be increasingly successful with increased temperatures and unsuccessful once temperatures fall below approximately 14°C. Monitoring water temperatures could limit wasted efforts in collecting snails with movement-based traps. Attempts to compare relative snail abundance will be confounded if temperatures vary between sampling sites or within a sampling site over time, especially if temperatures range from 10 to 20°C.

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