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The Anthropic Principle, String Theory, and Multiple Universes in Light of the Scientific Method

Jerome Goddard[1]
Mississippi Department of Health, Jackson, MS 39215

Epistemology is the study of the nature and grounds of knowledge, especially with reference to its limits and validity. There are two main goals of epistemology: (1) to find out as much truth as possible, and (2) to avoid as much falsehood as possible. These two goals are in tension with each other. In trying to understand the world, the ancient Greek philosophers diligently strove to develop a coherent and well-defined philosophy. Even though modern technology and scientific advancements seem to render the ancient Greeks silly, superstitious, or unenlightened, we are actually faced with the same challenge they were – to find a rational explanation of the universe.

There has been considerable debate lately in the physics community over an idea called the "anthropic cosmological principle" (Barrow and Tipler, 1986; Barrow, 2002; Susskind, 2003). According to this idea, the universe is made just right for life to occur. As one author puts it, "The universe must be suitable for life, otherwise we would not be here to wonder about it" (Overbye, 2003). There are numerous features and mathematical constants in the equations of physics and cosmology which do not seem predictable by any known theory, and which seem to be miraculously tuned to allow life. Any slight deviation from these settings would be disastrous, causing things like stars to collapse and atoms to evaporate. One of the most striking examples of the anthropic principle is the cosmological constant, a number that measures the amount of cosmic repulsion caused by the energy in empty space (Carroll and Press 1992). As predicted by quantum theory, empty space should be brimming with this energy. In fact, recent discoveries have shown that cosmic repulsion is indeed present and seems to be helping in the expansion of the universe. However, the observed cosmological constant (lambda) is perhaps as much as 1,000 times lower than its estimated value (Weinberg, 1989; Carroll and Press, 1992). So *why* is the cosmological constant what it is? Why is it different from that expected based upon mathematical formulas? It is at this point that people invoke the anthropic principle.

The anthropic principle is often used as a religious argument for special creation with reasoning like this, "The reason our universe is so peculiar and well-fitted to life is because the Creator wanted (willed) it to be that way for the formation of life." Dr. Steven Weinberg, a Nobel laureate from the University of Texas, puts it like this. "A person is dealt a royal flush in a poker tournament. It may be chance, but on the other hand, the organizer of the tournament may be our friend" (Overbye, 2003; Susskind, 2003).

One way to get around the anthropic principle is to theorize that there have been millions of possible universes throughout time, with many different constants and settings in each one ruled by chance, and/or that there are "regions" (bubbles) within our universe containing a variety of constants and settings. The reason we are here to observe this universe is because we happen to be in one of those multiple universes or perhaps bubbles within our universe conducive to formation of life. String theory provides some evidence to support this view.

String theory. String theory is the idea that fundamental particles of the universe – protons, neutrons, electrons, quarks, etc. – contain tiny vibrating, oscillating, dancing filaments called "strings." String theory adds a new microscopic layer (a vibrating loop) to the previously known progression (large to small) from atoms to protons, neutrons, electrons, and quarks (Greene 2003; Greene 2004) . No one has actually seen these strings; they are all theoretical at this point. According to the idea, everything in the universe is comprised of tiny vibrating fundamental strings. Moreover, every one of these strings is identical. The only difference between one string and another, whether it is a heavy particle part of an atom or a massless particle that carries light, is its resonant pattern, or how it vibrates (Greene, 2003).

[1]PO Box 1700, Jackson, MS 39215
601-576-7689; jgoddard@msdh.state.ms.us

String theory helps resolve the incompatibility between quantum mechanics and general relativity – the properties of forces vs. the properties of particles. For this reason, many physicists think string theory can become a "theory of everything" because it can underlie all others. A theory of everything – the ultimate explanation of the universe at its most microscopic level – would provide the firmest foundation on which to build our understanding of the world.

String theory allows for many dimensions (10 or 11; perhaps even more) in a space framework which could serve as a landscape containing peaks, valleys, and ridges (de Boer, 2003). As the universe expanded after the Big Bang, it theoretically rolled down, or over, this landscape framework. By chance, in some of these valleys small regions or pockets of universes (bubbles) might occur in which the natural constants and settings are conducive to life.

MULTIPLE UNIVERSES?

Scientific method. To accurately understand our world, scientists developed the scientific method. For a long time, the preferred scientific method was induction – basing general statements on accumulated observations of specific instances. For example, "Since the sun has arisen every day during recorded history, it is therefore true that the sun will rise tomorrow." Use of induction was helpful and enabled early scientists to distinguish science from non-science. However, David Hume in the mid-1700s pointed out that no number of singular observations, however large, could logically fix a general statement or law (Melchert, 1999). His skepticism may have seemed silly to laypeople, but actually unmasked a truth – pure empiricism is not a sufficient basis for science. We do not know for sure that the sun will rise tomorrow. It is highly probable that it will (in light of historical observations), but we do not know for sure.

A major shift in the scientific method occurred in the 1900s when Karl Popper advanced the idea that science should advance by trying to "falsify" hypotheses. Once falsified, they can either be amended, qualified, or adjusted and the process started over again. For example, the hypothesis, "all swans are white" can be supported by thousands of observations of white swans. But it is really not important how many observations agree with the theory; what really matters is trying to disprove the theory. One single observation of a black swan allows us to logically derive the statement, "Not all swans are white." In this way of looking at things, empirical generalizations, though not verifiable, are falsifiable. Under this new system, we can never prove that what we know is true; it is always possible that it will turn out to be false. The most you can ever say about a theory – be it gravity, Big Bang, evolution, etc – is that it is supported by every observation so far, and yields more precise predictions than any known alternative. However, it may be expanded or engulfed later by a better theory. For example, Einstein's theory of special relativity expands Newtonian mechanics (NM) to high velocities, but NM is still used.

A critical premise in Popper's method is that a theory must be testable. The hypothesis must lend itself to experiments or observations in efforts to disprove it. Taking the swan example (above), we must be able to go out and look at swans. If our theory about the color of swans relates to the color of swans in another universe, then that theory is untestable and thus lies outside the boundaries of science. We can discuss it, yes, but test it, no.

Multiple universes or pockets within our universe. As mentioned, one way to get around the anthropic principle is to theorize that there have been millions of possible universes, with many different constants and settings ruled by chance. Alternatively, string theory might allow for pocket universes or bubbles within our universe with a wide range of physical laws and constants. Accordingly, some small fraction of those bubbles would be within the anthropic window. And it is in one of these regions that we find ourselves (Susskind, 2003). Again, according to string theory, the only reason we are here to observe this universe or pocket within our universe is because we happen to be in one of them conducive to formation of life.

To me, proposing that ours is but one of a string of universes is a fallacy in reasoning. The universe is supposedly "everything there is." That is what the term universe means. If one tries to argue about things outside the universe or before the universe, an opponent usually quips, "that's outside the boundary of science. What lies outside the universe is an unknowable nothingness." Okay. Then how can an explanation for our universe being uniquely adapted for life be that ours is just one of many universes? There is no way to test such a statement.

The bubble idea suffers from the same flaw. Yes, string theory math might allow for such phenomena,

but there is no way to test such a claim. Dr. Leonard Susskind at Stanford says, "Direct observational confirmation of the vastness and diversity of the (universe) landscape is probably not possible. The space between bubbles is typically expanding so rapidly that no signals can reach one of them from any other" (Susskind, 2003).

Recall Popper's method of hypothesis testing (more accurately "falsifying"). In the case of the swans we can never say that all swans are white by counting white swans. But finding one black swan would answer the question. However, to test the hypothesis, we must be able to look at swans. There is no possible way to test the multiple universe hypothesis – or even the pocket-universes-within-our-universe hypothesis. As silly as it sounds, *all there is to observe is what there is to observe.* Yet the multiple universe response is often quoted when people discuss the anthropic principle. In my view, we would do well to learn from the ancient Greek philosophers how to keep our theory of knowledge consistent and coherent.

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Red-cockaded Woodpecker (*Picoides borealis*) Behavior in a Mississippi Loblolly-Shortleaf Pine Forest

Douglas R. Wood[1,2], L. Wesley Burger, Jr.[2], and Francisco J. Vilella[3]

[2]Department of Wildlife and Fisheries, Mississippi State University, Mississippi State, MS 39762, and [3]Mississippi Cooperative Fish and Wildlife Research Unit, Mississippi State, MS 39762

From 1997 to 1999, we characterized red-cockaded woodpecker (*Picoides borealis*) behavior in a loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pine forest in Mississippi. We recorded stem type and size class used, foraging location, height, first behavior type observed and cumulative behaviors during 5-hour visual observation periods of 41 red-cockaded woodpecker groups. Overall, 94% of all stems used by red-cockaded woodpeckers were pines, whereas only 6% of stems used were hardwoods. However, use of hardwood stems increased during the nonbreeding season. Red-cockaded woodpeckers selected large pine stems (= 47.5 cm) compared to hardwood stems (= 33 cm). During all seasons, red-cockaded woodpeckers foraged predominantly within the crown and high-trunk area of trees. Foraging and group cohesion behaviors were performed during all seasons, however foraging behaviors increased during the nonbreeding season.

Red-cockaded woodpeckers (*Picoides borealis*) (RCW) are a federally-endangered species endemic to mature longleaf (*Pinus palustris*), loblolly (*P. taeda*), and shortleaf (*P. echinata*) pine forests of the southeastern United States (Jackson, 1994). RCWs are bark-probing insectivores that exhibit sexual segregation during foraging (Ligon, 1970; Jackson, 1994); however, most studies have been conducted in longleaf pine forests (Morse, 1972; Engstrom and Sanders, 1997). RCWs frequently use a foraging strategy known as scaling or flaking to obtain prey (Ligon, 1968). Feet or bills are used to remove large flakes of bark to reveal prey. Ligon (1968, 1970) also reported flycatching and foliage gleaning by RCWs.

Adults typically forage on ants (*Crematogaster* and *Camponotus* spp.), spiders (Araneae), wood roaches (*Parcoblatta* spp.), beetle larvae and other invertebrates (Beal, 1911; McFarlane, 1995; Hess and James, 1998). RCWs may shift their diet to include more larvae during winter (Hess and James, 1998). In South Carolina, RCW nestlings were fed insect larvae, wood roaches, spiders, ants and centipedes (*Scolopendromorpa* spp.) (Harlow and Lennartz, 1977; Hanula and Franzreb, 1995). RCWs also have been documented foraging in slash piles on the ground (Ligon, 1970). RCWs obtain water directly from puddles or metabolically prey (Ligon, 1970; Jackson, 1994).

RCWs frequently use large diameter pine trees (Jackson, 1994); however, Ramey (1980) documented greater percentages of hardwoods selected by foraging RCWs in Mississippi and South Carolina. Although RCWs prefer pines for foraging rather than hardwoods (Jackson, 1994), landscape and regional context may play a role in the frequency of hardwood selection. Subpopulations in the eastern portion of the RCWs range inhabit longleaf pine ecosystems with low densities of hardwoods, typically found in riparian areas or stream-side management zones. However, RCW subpopulations in the central and western portion of the species' range inhabit loblolly and shortleaf pine ecosystems with greater densities of hardwoods. These areas frequently have increased hardwood densities throughout the landscape that are not restricted to riparian areas.

This research was conducted as part of a broader study of RCW foraging ecology and reproductive success (Wood, 2001). Our objectives were to characterize RCW foraging behavior, including stem use and type, relative location and height selection, first behavior type, and cumulative behaviors in a loblolly and shortleaf pine forest.

[1]Author for correspondence: Department of Biological Sciences, Southeastern Oklahoma State University, 1405 N. 4th Ave., PMB 4068, Durant, Oklahoma 74701–0609; dwood@sosu.edu

MATERIALS AND METHODS

Research was conducted at the Bienville National Forest (BNF) in central Mississippi. BNF consists of 72,216 ha of pine, pine-hardwood, and hardwood stands in a fragmented landscape (Wood, 2001). Dominant tree species include loblolly, longleaf, and shortleaf pine. Common hardwood species include white oak (*Quercus alba*), post oak (*Q. stellata*), southern red oak (*Q. falcata*), mockernut hickory (*Carya tomentosa*), sweetgum (*Liquidambar styraciflua*), and winged elm (*Ulmus alata*).

From 1997 to 1999, we characterized foraging and other behaviors of 41 RCW groups. Jackson (1994) defined an RCW group as the brood pair and ≥ 1 related RCWs which are usually sons of the brood pair. Each year, 12–15 RCW groups were randomly-selected without replacement for intensive monitoring from the population of 95 active groups at BNF. Overall, approximately 1925 hours of observations were recorded for 41 different RCW groups. Five-hour visual observation periods were performed on each group for one year beginning in January and concluding in December. Observation periods were performed daily and sequentially by group throughout the year to approximate equal effort. Each observation period began at first light and continued for five hours (Engstrom and Sanders, 1997). The breeding season was defined as 7 April–31 July and the nonbreeding season as 1 January–6 April and 1 August–15 December (Jackson, 1994). Each observation period was subdivided into 6-min periods consisting of a 1-min observation period followed by a 5-min waiting period when no data were collected (Hooper et al., 1982; DeLotelle et al., 1983). During the 5-hour observation period, as many 6-min periods as possible were recorded (Brennan and Morrison, 1990).

RCWs forage as a group, thus we defined the group as the sampling unit for characterizing behaviors (Sherrill and Case, 1980; Hooper et al., 1982; Doster and James, 1998). Individuals were classified by age (e.g., juvenile males can be identified by a red patch of feathers on the crown of the bird) and sex when possible, however identification proved difficult due to dense midstory vegetation and we were not able to color-mark all RCWs. During 1-min observation periods, one RCW from the group was observed and all locations of that individual were spot-mapped on graph paper and subsequently each RCW location was georeferenced with a differentially-corrected global positioning system unit.

We recorded the species of tree and the diameter at breast height (dbh) of each stem used for foraging. We also recorded an individual RCW's location on the tree within one of three relative location categories (i.e., trunk within the crown, trunk below the crown, or limbs) (Ligon, 1968). Each location on the tree was assigned a relative height category (i.e., lower third, middle third or higher third) within location categories (Wood, 2001). Thus, each location was assigned to a location-height category (e.g., low-crown or high-trunk).

We recorded the cumulative number and type of behaviors (Table 1) performed during 1-min observation periods (Kilham, 1959; Ligon, 1970; Kilham, 1974). We also recorded the behavior performed at the first second of 1-min observation periods, hereafter referred to as first behavior, that provided an independent sample of behavior compared to cumulative behavior counts. First behavior data were only collected in 1998 and 1999 as a modification from the original protocol performed in 1997 (Wood, 2001).

We used SAS version 7.0 for all statistical analyses ($\alpha = 0.05$) (SAS Institute 1998). We tested the hypothesis that the number of pine and hardwood stems used by foraging RCWs was equal among groups and seasons. We used a log-linear analysis to examine the 3-way interaction terms of group, season, and stem type. Chi-square tests were used to test for differences between seasons and stem types, as well as differences between groups and stem types. We also tested the hypothesis that dbh of pine and hardwood stems used by foraging RCWs was equal. Within pine and hardwood classes, we tested the hypothesis that there were no differences in dbh between seasons. We used unbalanced, mixed-model ANOVAs to test for effects of group, year, season, and stem type on dbh of stems used by foraging RCWs.

Chi-square tests of homogeneity were used to test the null hypothesis that RCWs used similar location-height categories on foraging stems annually and during the breeding and nonbreeding season. We used equal prior probabilities because previous studies conflicted on RCW foraging locations (Ligon, 1970; Morse, 1972). Because our study design was observational, we made no attempt to test location-height observations with availability of these categories among various stem types used. For first behavior analysis, we used PROC GENMOD on the actual counts of first behavior for all RCW groups combined annually and during the breeding and non-

Table 1. Red-cockaded woodpecker (*Picoides borealis*) behaviors observed at Bienville National Forest, Mississippi 1997–1999.

Behavior	Definition
Foraging	Actively capturing prey, scaling, flaking, probing
Hunting	Actively searching a substrate
Calling	Vocalizing
Loafing	Motionless on a substrate
Preening	Arranging or smoothing plumage
Cavity maintenance	Drilling resin wells near cavity; not excavating inside a cavity
Drumming	Tapping on substrate for communication; not drilling resin wells
Fed nestling	Providing food to a nestling
Fed fledgling	Providing food to a recently-fledged offspring
Cavity excavation	Actively excavating inside a cavity
Wing display	Raised wings above body
Scratching	Using toes to scratch
Play/social interaction	Intragroup chases, territorial behavior, dominance behaviors

breeding season. If a year effect was detected, years were analyzed separately.

RESULTS

Stem use. Loblolly and shortleaf pine accounted for 99% of all foraging observations on pines, whereas post oak, white oak, winged elm, southern red oak, and sweetgum accounted for 82% of hardwoods selected by foraging RCWs (Table 2). RCWs anecdotally were observed foraging on eight tree species (spruce pine [*P. glabra*], American beech [*Fagus grandifolia*], black cherry [*Prunus serotina*], blackjack oak [*Q. marilandica*], pignut hickory [*Carya glabra*], sassafras [*Sassafras albidum*], sugarberry [*Celtis laevigata*], and swamp chestnut oak [*Q. michauxii*]), but were not recorded during 1-min observation periods.

Annually and during the breeding season, RCWs foraged more frequently on pines than hardwoods (Table 3). However, we observed an increase in hardwood use compared to pines during the nonbreeding season (Table 3). RCWs foraged more frequently on hardwoods during the nonbreeding season than the breeding season ($\chi_1^2 = 31.3$, $P < 0.001$). Stem type use by RCWs varied between seasons ($\chi_1^2 = 38.7$, $P < 0.001$) and among groups ($\chi_{40}^2 = 242.5$, $P < 0.001$).

Stem diameter. Foraging RCWs frequently used large diameter pines and, less frequently, large diameter hardwoods (Table 4). No year effect was detected ($F_{2,38} = 2.03$, $P = 0.15$), however dbh of pines was greater than hardwoods ($F_{1,9703} = 770.09$, $P < 0.001$) for the breeding and nonbreeding seasons. A difference in dbh between seasons ($F_{1,9703} = 27.47$, $P < 0.001$) was detected for pines and hardwoods.

Location-height. Annually, RCWs were observed more frequently on the trunk and limbs within the crown than on the trunk below the first limb ($\chi_1^2 = 2895$, $P < 0.001$) (Table 5). RCWs were more frequently observed on the trunk within the crown than on the trunk below the crown and on limbs ($\chi_2^2 = 3098$, $P < 0.001$). In ranked order, RCWs foraged more frequently in the mid-crown, low-crown, high-crown, and high-trunk areas of foraging stems ($\chi_8^2 = 5016$, $P < 0.001$) (Table 5).

During the breeding season, RCWs were observed more frequently on the trunk and limbs within the crown than on the trunk below the first limb ($\chi_1^2 = 408$, $P < 0.001$). RCWs also were more frequently observed on the trunk within the crown than on the

trunk below the crown and on limbs (χ_2^2 = 636, $P < 0.001$). RCWs foraged more frequently on the high-trunk and mid-crown areas of trees than other areas (χ_8^2 = 1627, $P < 0.001$) (Table 5).

During the nonbreeding season, RCWs were observed more frequently on the trunk within the crown and limbs within the crown than on the trunk below the first limb (χ_1^2 = 2959, $P < 0.001$). RCWs also were observed more frequently on the trunk within the crown than on the trunk below the crown and on limbs (χ_2^2 = 3183, $P < 0.001$). RCWs foraged more frequently in the mid-crown and high-crown areas of trees (χ_8^2 = 4371, $P < 0.001$) (Table 5).

First behavior. A year by season interaction effect (χ_1^2 = 55.0, $P < 0.001$) was detected for first behavior, thus years were analyzed separately (Table 6). In 1998 and 1999, preening, cavity maintenance, drumming, fed nestling, fed fledgling, excavation, wing display, scratching, and play behaviors were not performed frequently enough to permit meaningful analysis (Table 6). During 1998, foraging (χ_1^2 = 183.5, $P < 0.001$), hunting (χ_1^2 = 98.9, $P < 0.001$), calling (χ_1^2 = 9.8, P = 0.002), and loafing (χ_1^2 = 23.8, $P < 0.001$) were performed more during the nonbreeding season than the breeding season, however variation existed among groups for foraging (χ_{13}^2 = 175.8, $P < 0.001$), hunting (χ_{13}^2 = 90.5, $P < 0.001$), calling (χ_{13}^2 = 24.0, P = 0.03), and loafing (χ_{13}^2 = 27.4, P = 0.011). During 1999, foraging (χ_1^2 = 0.23, P = 0.63), calling (χ_1^2 = 0.62, P = 0.43), and loafing (χ_1^2 = 0.88, P = 0.35) were not different between seasons, however variation was detected among groups for foraging (χ_{11}^2 = 59.9, $P < 0.001$), calling (χ_{11}^2 = 31.7, P = 0.001), and loafing (χ_{11}^2 = 25.0, P = 0.01). Hunting (χ_1^2 = 72.2, $P < 0.001$) was performed more frequently during the nonbreeding season than the breeding season, however variation was detected among groups (χ_{11}^2 = 72.7, $P < 0.001$).

Table 2. Number and percent of pine and hardwood species used by foraging red-cockaded woodpeckers (*Picoides borealis*) at Bienville National Forest, Mississippi 1997–1999.

Stem type	Number	%
Pine		
Loblolly Pine (*Pinus taeda*)	8082	88.0
Shortleaf Pine (*P. echinata*)	1005	11.0
Pine Snag (*Pinus* spp.)	67	0.5
Longleaf Pine (*P. palustris*)	50	0.5
Total	9204	100.0
Hardwood		
Post Oak (*Quercus stellata*)	141	26.0
White Oak (*Q. alba*)	92	17.0
Winged Elm (*Ulmus alata*)	91	17.0
Southern Red Oak (*Q. falcata*)	70	12.0
Sweetgum (*Liquidambar styraciflua*)	56	10.0
Mockernut Hickory (*Carya tomentosa*)	28	5.0
Hardwood Snag	23	4.0
Northern Red Oak (*Q. rubra*)	17	3.0
Water Oak (*Q. nigra*)	7	1.0
Willow Oak (*Q. phellos*)	7	1.0
Black Gum (*Nyssa sylvatica*)	6	1.0
Flowering Dogwood (*Cornus florida*)	2	0.5
Shagbark Hickory (*Carya ovata*)	2	0.5
White Ash (*Fraxinus americana*)	1	0.5
Red Maple (*Acer rubrum*)	1	0.5
Yellow Poplar (*Liriodendron tulipifera*)	1	0.5
Total	545	100.0

Table 3. Number, mean percent, and range of percentage of stem type used by red-cockaded woodpeckers (*Picoides borealis*) at Bienville National Forest, Mississippi 1997–1999.

Season	Stem type	Number of stems	%	Range %
Annual	Pine	9204	94	83–100
	Hardwood	545	6	0–17
Breeding Season	Pine	4459	96	86–100
	Hardwood	187	4	0–14
Nonbreeding Season	Pine	4742	93	69–100
	Hardwood	361	7	0–31

Table 4. Mean (± SE) dbh (cm) of pine and hardwood stems used annually and seasonally by foraging red-cockaded woodpeckers (*Piciodes borealis*) at Bienville National Forest, Mississippi 1997–1999.

Year	Season	Type	Number of stems	$\bar{x}$ ± SE
1997	Breeding	Pine	1737	48.3 ± 0.3
		Hardwood	99	35.1 ± 1.6
	Nonbreeding	Pine	1131	46.5 ± 0.4
		Hardwood	151	32.3 ± 0.9
1998	Breeding	Pine	1739	45.2 ± 0.3
		Hardwood	72	30.0 ± 1.7
	Nonbreeding	Pine	2438	47.5 ± 0.3
		Hardwood	185	31.0 ± 1.1
1999	Breeding	Pine	983	47.2 ± 0.4
		Hardwood	16	33.0 ± 3.6
	Nonbreeding	Pine	1173	51.5 ± 0.3
		Hardwood	25	43.5 ± 2.1
1997–1999	Breeding	Pine	4459	47.0 ± 0.3
		Hardwood	187	33.0 ± 0.8
	Nonbreeding	Pine	4742	48.3 ± 0.3
		Hardwood	361	32.5 ± 1.0

Table 5. Percent of red-cockaded woodpecker (*Picoides borealis*) observations (*n* = 11,165) by location-height categories annually and seasonally at Bienville National Forest, Mississippi 1997–1999.

	Breeding season	Nonbreeding season	Annual
Crown-high	11.7	18.4	15.3
Crown-mid	20.0	32.3	26.7
Crown-low	14.7	16.7	15.8
Trunk-high	21.4	10.3	15.4
Trunk-mid	11.0	3.6	6.9
Trunk-low	3.4	1.2	2.2
Limbs-high	3.3	5.2	4.3
Limbs-mid	9.2	9.5	9.5
Limbs-low	5.3	2.8	3.9

DISCUSSION

At BNF, RCWs frequently used pines for foraging activities. Zwicker and Walters (1999) reported that 94% of all RCW foraging stems were pines and were used in greater proportion than availability. In Louisiana, RCWs selected pines greater than their availability (90% use; 64% available), whereas hardwoods were selected less than their availability (Jones and Hunt, 1996). During the breeding season, RCWs in Louisiana foraged more frequently on smaller pine stems (< 40 cm dbh) than during the nonbreeding season (Jones and Hunt, 1996).

In Arkansas, Doster and James (1998) documented 95% foraging on shortleaf pines compared to 5% hardwoods. In Mississippi and South Carolina, Ramey (1980) reported 78–94% foraging on pines. However, higher rates of foraging on pines is frequently reported from longleaf forests which are more homogenous in terms of composition. In Florida, Porter and Labisky (1986) reported 99% foraging on pine stems and Hardesty et al. (1997) reported 97% of stems used by foraging RCWs were pines.

We observed some of the highest rates of hardwood stem selection by RCW groups, particularly during the nonbreeding season, compared to the literature (Skorupa and McFarlane, 1976; Ramey, 1980). For example, 31% of all stems used by one RCW group were hardwoods in 1999. BNF, in the West Gulf Coastal Plain, has an increased hardwood component compared to longleaf systems in the southeastern portions of the RCWs' range (Rudolph and Conner, 1996). Thus, more hardwoods were potentially available in the overstory for foraging activities. Increased hardwood use during the nonbreeding season also may be due to social dominance. Jones and Hunt (1996) suggested dominance and sexual segregation may pressure juvenile RCWs lower on pines or onto nearby hardwoods. We also observed juvenile male RCWs foraging on smaller dbh hardwoods such as winged elm and sweetgum.

Skorupa and McFarlane (1976) reported that RCWs in South Carolina did not forage on hardwoods in summer. However, 10% of all RCW foraging stems in winter were hardwoods; suggesting that decreasing winter prey availability in pine stands may increase the use of hardwoods by RCWs (Skorupa and McFarlane, 1976). In Florida, DeLotelle et al. (1987) also reported a seasonal increase in the use of hardwood stems by RCWs. They foraged on baldcypress (*Taxodium distichum*) in greater proportion than availability during the nonbreeding season (DeLotelle et al., 1987).

Hardwood species selected by RCWs at BNF, such as white oak, post oak and southern red oak, have deeply-grooved or loose bark that may appear texturally similar to pine substrates used by RCWs. An alternate hypothesis may be that RCWs forage on hardwoods due to increased invertebrate availability compared to pine stems. Hardwoods may harbor more invertebrates than pines during winter months, especially after invertebrates have been depleted from nearby pines by a central-place forager like the RCW (Skorupa and McFarlane, 1976; DeLotelle et al., 1987). However, other bark-probing woodpecker species may exclude RCWs from hardwoods. During our study, we observed red-bellied woodpeckers (*Melanerpes carolinus*), red-headed woodpeckers (*M. erythrocephalus*), and downy woodpeckers (*P. pubescens*) displace RCWs from hardwoods.

Table 6. Mean number (± SE) of first behaviors of red-cockaded woodpecker (*Picoides borealis*) groups annually and seasonally at Bienville National Forest, Mississippi 1998–1999.

Year	Behavior	Breeding season	Non-breeding season	Annual
1998	Foraging	50.1 ± 5.2	93.1 ± 9.2	71.6 ± 6.6
	Hunting	43.4 ± 4.3	71.7 ± 5.7	57.5 ± 4.5
	Calling	9.5 ± 1.2	13.5 ± 1.5	11.5 ± 1.0
	Loafing	11.0 ± 1.6	5.71 ± 1.0	8.36 ± 1.1
	Preening	2.86 ± 0.6	1.0 ± 0.3	1.93 ± 0.4
	Cavity maintenance	2.57 ± 0.8	0.86 ± 0.4	1.71 ± 0.5
	Drumming	0.21 ± 0.1	0.0	0.11 ± 0.1
	Fed nestling	0.43 ± 0.4	0.0	0.21 ± 0.2
	Fed fledgling	0.5 ± 0.4	0.0	0.25 ± 0.2
	Cavity excavation	6.1 ± 3.0	0.0	3.04 ± 1.6
	Wing display	0.07 ± 0.1	0.0	0.04 ± 0.1
	Scratching	0.07 ± 0.1	0.0	0.04 ± 0.1
	Play	0.57 ± 0.2	0.0	0.29 ± 0.1
1999	Foraging	39.9 ± 3.3	41.2 ± 5.1	40.5 ± 3.0
	Hunting	18.8 ± 2.6	37.0 ± 4.6	27.9 ± 3.2
	Calling	27.9 ± 1.0	26.3 ± 3.1	27.1 ± 1.6
	Loafing	6.17 ± 1.1	5.25 ± 0.8	5.71 ± 0.7
	Preening	0.75 ± 0.3	0.42 ± 0.2	0.58 ± 0.2
	Cavity maintenance	1.17 ± 0.6	1.17 ± 0.9	1.17 ± 0.5
	Drumming	0.08 ± 0.1	1.42 ± 0.8	0.75 ± 0.4
	Fed nestling	2.33 ± 0.6	0.0	1.17 ± 0.4
	Fed fledgling	0.67 ± 0.3	0.0	0.33 ± 0.2
	Cavity excavation	1.92 ± 0.8	0.0	0.96 ± 0.5
	Wing display	0.25 ± 0.2	0.08 ± 0.1	0.17 ± 0.1
	Scratching	0.0	0.0	0.0
	Play	0.0	0.08 ± 0.1	0.04 ± 0.1

Stem diameter. Mean dbh of pines used by RCWs at BNF were similar to mean dbhs reported in other loblolly-shortleaf pine forests. In a mixed Louisiana forest, > 50% of pines selected by foraging RCWs ranged from 40–60 cm dbh, which was greater than their availability (Jones and Hunt, 1996). Further, pines < 40 cm dbh were selected more during the breeding season than the nonbreeding season (Jones and Hunt, 1996). In an Arkansas shortleaf forest, Doster and James (1998) documented that 75% of all RCW foraging stems were ≥ 30.5 cm dbh, although no stems > 38 cm dbh were available on their site. Doster and James (1998) also observed RCWs foraging on stems as small as 7.6–15.2 cm dbh.

Hardesty et al. (1997) reported a mean dbh of 29.7 cm for stems selected by RCWs in a Florida longleaf pine forest. They reported a wide range of longleaf pine size classes, similar to BNF, used by RCWs (3.2–72.4 cm). In a North Carolina longleaf forest, Zwicker and Walters (1999) reported that the majority of stems selected by RCWs ranged from 20.1–35.0 cm. Similarly, pines ≥ 25.1 cm dbh were used more than their availability and 5.1–25.0 cm dbh pines were used less than their availability (Zwicker and Walters, 1999).

In an old-growth longleaf pine forest, Engstrom and Sanders (1997) reported that 80% of pines used by RCWs ranged from 35–65 cm. Pines >31 cm were used greater than their availability, whereas stems < 20 cm were used less than their availability (Engstrom and Sanders, 1997). In a Florida longleaf forest, DeLotelle et al. (1983) reported that RCWs preferred pines ≥ 27 cm dbh. However, DeLotelle et al. (1983) also reported extensive use of smaller age classes (12–16 cm). Small pines accounted for 27% of the stems available, but incurred 31% use by RCWs. Thus, foraging on smaller dbh stems is not limited to RCW subpopulations in loblolly-shortleaf pine systems.

Location-height. We characterized general patterns in location and height by foraging RCWs, although we were unable to obtain enough data to analyze differences between males and females. Previous studies have documented sexual segregation and resource partitioning by RCWs in longleaf pine forests (Engstrom and Sanders 1997), however we were unable to document similar results in a loblolly-shortleaf pine forest. Annually, and for both seasons, RCWs foraged on the trunk above the first limbs and on limbs. Our results may reflect the presence of male helpers and juveniles in RCW groups with > 2 members, thus the increase in foraging observations on the trunk above the first limbs and on limbs. Ramey (1980) documented that males and females preferred foraging on trunks, but males foraged more on limbs than females in a Mississippi loblolly pine forest. In an old-growth longleaf pine forest, Engstrom and Sanders (1997) documented a similar pattern of resource partitioning in RCWs: males foraged more on the upper trunk and limbs, whereas females foraged on the trunk below the first limbs. RCWs segregated further by foraging substrate as well, with females concentrating on bark-probing whereas males used a diversity of food sources (Engstrom and Sanders, 1997).

Behavior. RCWs at BNF allocated the majority of their behaviors to foraging and group cohesion maintenance (e.g., calling). The trend towards increased time spent foraging was more evident during the nonbreeding season when food availability declines and the need for thermoregulation increases with decreased ambient temperatures. During the breeding season, RCWs at BNF performed more behaviors related to reproductive activities such as cavity excavation, copulation, and feeding offspring.

We observed several interesting foraging behaviors during our study. In the summer of 1998, RCWs took advantage of a cicada outbreak. RCWs would sally from a tree, catch a cicada in flight, return to the same tree and ingest the insect. On several occasions, we observed RCWs foraging for insects on deadfall and drinking from puddles on the ground similar to observations by Ligon (1970) and Jackson (1994).

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Consumer Preference of Apples Grown in Northern Mississippi[1]

Maria J. Sindoni[2], Frank B. Matta[3,4], and Juan L. Silva[5]

[2]Instituto National de Investigacion Agropecuaria (INIA)- Anzoátegui, Venezuela;
[3]Department of Plant and Soil Sciences, Mississippi State University, Mississippi State, MS 39762; and
[5]Department of Food Science and Technology, Mississippi State University, Mississippi State, MS 39762

Apples of cultivar/rootstock combination 'Earligold'/EMLA 7, 'Jonagold'/EMLA 111, 'Improved Golden'/EMLA 7, 'Improved Golden'/EMLA 111, 'Scarlet Gala'/EMLA 7, 'Jonafree'/Mark, 'Macspur'/M7A, 'Royal Gala'/MM 111, and 'William's Pride'/M7A were evaluated by an untrained consumer panel at harvest, 30 days, and 60 days after harvest. Changes in apple appearance, flavor, sweetness, tartness, and firmness were rated. All combinations except 'Jonafree'/Mark and 'Macspur'/M7A had a high acceptance rating by the panelists during the study. Fruit of 'Earligold'/EMLA 7 and 'William's Pride'/M7A had a moderate acceptance by the panelists at harvest. Results indicated that fruit of medium and late cultivars such as 'Improved Golden'/EMLA 7, and 'Royal Gala'/ MM111 were preferred by panelists compared to fruit of the early harvested cultivars 'Earligold'/EMLA 7 and 'William's Pride'/ M7A.

The consumer traditionally plays a major role in determining fruit acceptability for marketing of fresh and stored fruit (Wills et al., 1998). Consumers' perception of apple quality include such factors as appearance, texture, firmness, sweetness, and flavor with preference and taste being key factors affecting consumer purchase decisions. Growers can improve product attributes, competitiveness, and marketability by using knowledge of consumers demand (Brumfield et al., 1993). Watkins et al. (1993) indicated that in 'York Imperial,' apple fruit firmness and soluble solid contents (SSC) were the best indicators of fruit maturity and quality. Optimal quality for Washington apples was obtained for fruit harvested 173 to 180 days after full bloom (Plotto et al., 1995). In addition to maintaining high quality standards, good storage life is essential in successful marketing and selling of fruit to consumers (Patte, 1985). Researchers have found that apples can be stored from -1 °C and 4 °C for 90 days while maintaining quality (Westwood, 1993). Johnson and Ertan (1983) reported that 'Idared' apples stored at 1 °C were firmer than those kept at 0 °C or 4 °C. Shelf life after storage is also an important aspect of cultivar evaluations (Moore and Ballington, 1990). It is important to evaluate apple cultivar acceptance both at harvest and after storage. Many scientists have used taste panels to determine quality of apples and most studies are concerned with preferences or differences among cultivars (Watada et al., 1980). Plotto et al. (1997) and Williams and Langron (1983) have used sensory science such as hedonic scales or intensity scales to describe apple cultivars. Since the taste evaluations of Janson (1972), little has been published in North America on taste ratings of apples, especially the newer cultivars. In addition, there is little information on which parameters to use in measuring consumer preference of apples. Apples have many divergent attributes that are associated with acceptability and/or desirability (Watada et al., 1980). Williams and Langron (1983) conducted a study of attributes that panelists recognized in 'Cox's Orange Pippin' apples and concluded that quality of apples can be characterized best by identifying the significant attributes, and then determining the intensity of such attributes. The purpose of this study was to determine consumer preference for apples based on appearance, flavor, sweetness, tartness, and firmness of fruit at harvest, and after harvest storage.

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[4]Author for Correspondence: Box 9555, 117 Dorman Hall; Fmatta@pss.msstate.edu

MATERIALS AND METHODS

Trees producing fruit for the experiment were seven years old and grown in Atwood silt loam soil at the Pontotoc Ridge-Flatwoods Research and Extension Center (38°08 N, 89°00' W), located seven miles south of Pontotoc, MS. The average annual maximum temperature of this area is 30 °C (86 °F) and minimum temperature is -1 °C (30 °F), with annual rainfall of 81.23 cm (32 inches). Research trees were planted in 1993 at a spacing of 2.5 m in rows and 3.7 m between rows. Trees were pruned to a modified central leader system. The soil pH was 5.6. In May 1999, a 5-20-20 fertilizer was applied at a rate of 450 g per tree, and ammonium nitrate (34-0-0) at a rate of 230 g per tree. No irrigation was applied. Weeds were controlled in the row by application of Round-up® herbicide in a one meter strip, and a mowed strip was maintained between rows. Insects and diseases were controlled through a spray program as recommended by Mississippi State University Extension Service.

Fruit from cultivar/rootstock combinations 'Earligold'/EMLA 7, 'Jonagold'/EMLA 111, 'Improved Golden'/EMLA 7, 'Improved Golden'/EMLA 111, 'Scarlet Gala'/EMLA 7, 'Jonafree'/Mark, 'Macspur'/M7A, 'Royal Gala'/MM 111, and 'Williams Pride'/M7A were included in this study. The experiment consisted of four single tree replications. Fruit quality and sensory evaluations were conducted immediately after harvest, 30 days, and 60 days after storage at 2 °C and 71% relative humidity (RH). Parameters evaluated were fruit size, expressed as fruit length and diameter, soluble solids content (SSC), juice pH, and firmness. Fruit size was measured using a vernier caliper and fruit firmness was measured using a penetrometer (Instron Universal Machine, Model 1011, Canton, MA) and measured in Newtons. Juice soluble solids content was measured in Brix with a Bausch & Lomb Abbe 3 L refractometer, and juice pH was measured using an Accumet pH meter 925 (Fisher Scientific, Pittsburgh, PA).

Five apples from each tree were washed and cut longitudinally and placed on paper plates for panelists to evaluate. A whole apple was also placed on the plate to be evaluated. Twenty-four people among students and staff were chosen at random from Dorman Hall, Plant and Soil Science Department, at Mississippi State University to participate in the test. Each panelist rated the apples for appearance, flavor, sweetness, tartness, and firmness using a ten point scale, where 1 = dislike extremely (very low), 5 = neither like or dislike (moderate), and 10 = like extremely (very high).

A completely randomized design with repeated measures was used in the experiment. Data were analyzed using PROC GLM (SAS Statistical Software, SAS Institute, Gary, N.C.). Treatment means were separated by LSD, 5% significance level.

RESULTS AND DISCUSSION

At harvest, consumer preference based on fruit appearance did not vary among cultivar/rootstock combinations, except for 'Macspur'/M7A which was least preferred (Table 1). Thirty days after storage, consumer preference for 'Earligold'/EMLA7 and 'Macspur'/M7A, was least. Fruit appearance among the remaining cultivar/rootstock combinations did not differ (Table 2). Sixty days after storage, 'Jonafree'/Mark and 'Macspur'/M7A were least preferred and 'Earligold'/EMLA7 and 'William's Pride'/M7A had completely deteriorated, hence the sensorial test for appearance of these cultivars was not possible. Consumer preference based on appearance among the remaining cultivars did not differ and ranged from 6.6 to 7.3 (Table 3). Similarities in preference among most of the cultivars suggest that panelists were consistent in rating the apples. Kappel et al. (1992) reported that in a sensory evaluation, only the visual attributes were found to be significantly different among the strains of 'Gala' and 'Jonagold.' Fruit appearance will be influenced by the intended market and this should be considered when selecting a cultivar for commercial production. Brumfield et al. (1993) reported similar conclusions when looking at consumer tastes and preferences in purchasing fresh tomatoes.

At harvest, consumer preference based on flavor indicated a high preference for 'Jonagold'/EMLA111, and 'Improved Golden'/EMLA7. These combinations were harvested mid and late season. The least preferred by the panelists were 'Jonafree'/Mark and 'Macspur'/M7A. Flavor did not differ among the remaining cultivar/rootstock combinations (Table 1). Thirty days after storage, 'Jonagold'/EMLA111 and 'Improved Golden'/EMLA7 maintained the highest preference rating by the panelists and 'Jonafree'/Mark and 'Macspur'/M7A, the lowest rating (Table 2). Sixty days after storage, 'Earligold'/EMLA7 and 'William's Pride'/M7A could not be tested due to fruit deterioration (Table 3). Similar results were reported by Plotto et al.

(1997) where distribution of sensory scores suggested that early harvested fruit had not developed full flavor and that high values for tartness and firmness did not necessarily imply quality and consumer acceptance.

At harvest, consumer preference based on sweetness indicated that 'Earligold'/EMLA7, 'Jonafree'/Mark and 'Macspur'/M7A were the least preferred by the panelists (Table 1). Thirty days after storage, 'Earligold'/EMLA7, 'Jonafree'/Mark, 'Macspur'/M7A, and 'William's Pride'/M7A were least preferred (Table 2). Sixty days after storage, the highest preference rating were for 'Improved Golden'/EMLA7 followed by 'Jonafree'/Mark, 'Jonagold'/EMLA111, 'Royal Gala'/MM111 and 'Scarlet Gala'/EMLA7, while 'Improved Golden'/EMLA111, 'Jonafree'/Mark, and 'Macspur'/M7A were least preferred. 'Earligold'/EMLA7 and 'William's Pride'/M7A were not tested due to fruit deterioration (Table 3).

Table 1. Panelists' ratings of various sensory parameters as influenced by cultivar at harvest, 1999.

	Parameter[y]				
Cultivar	Appearance	Flavor	Sweetness	Tartness	Firmness
'Earligold'/EMLA7	7.8 a[x]	6.0 c	5.2 bc	5.6 bcd	4.0 c
'Jonagold'/EMLA111	8.0 a	8.0 a	7.1 a	7.2 a	7.5 a
'Improved Golden'/EMLA7	8.0 a	8.0 a	7.5 a	7.3 a	8.0 a
'Improved Golden'/EMLA111	8.0 a	7.0 b	6.9 a	5.9 bc	7.5 a
'Scarlet Gala'/EMLA7	8.0 a	7.0 b	5.9 a	6.4 ab	7.5 a
'Jonafree'/Mark	8.0 a	5.5 d	5.3 bc	5.1 d	5.1 b
'Macspur'/M7A	6.8 b	5.6 d	5.5 b	5.3 b	5.3 b
'Royal Gala'/MM111	8.0 a	7.5 ab	6.8 a	6.8 ab	8.0 a
'William's Pride'/M7A	8.0 a	6.5 bc	6.7 a	6.0 bc	7.0 a

[x]Means in columns separated by Duncan's Multiple Range Test, $P < 0.05$. Means with the same letter do not differ

[y]Parameters were rated on a 10 point scale, where 1 = dislike extremely, and 10 = like extremely

Table 2. Panelists' ratings of various sensory parameters as influenced by cultivar at 30 days storage time, 1999.

	Parameter[y]				
Cultivar	Appearance	Flavor	Sweetness	Tartness	Firmness
'Earligold'/EMLA7	5.5 b[x]	5.9 b	4.4 c	4.5 c	4.5 c
'Jonagold'/EMLA111	7.5 a	7.6 a	6.7 a	6.8 a	6.8 a
'Improved Golden'/EMLA7	7.5 a	7.8 a	7.3 a	7.1 a	7.1 a
'Improved Golden'/EMLA111	6.6 a	6.9 b	6.8 a	5.9 bc	6.9 a
'Scarlet Gala'/EMLA7	7.5 a	6.7 b	6.5 a	6.0 ab	6.0 ab
'Jonafree'/Mark	7.0 a	5.0 c	5.0 b	4.4 c	5.4 b
'Macspur'/M7A	5.5 a	5.2 c	5.0 b	4.8 cd	5.0 b
'Royal Gala'/MM111	7.0 a	7.0 ab	6.7 a	6.2 ab	7.2 a
'William's Pride'/M7A	6.6 a	5.9 b	5.4 b	4.8 c	4.8 c

[x]Means in columns separated by Duncan's Multiple Range Test, $P < 0.05$. Means with the same letter do not differ

[y]Parameters were rated on a ten point scale, where 1 = dislike extremely, and 10 = like extremely

Table 3. Panelists' ratings of various sensory parameters as influenced by cultivars at 60 days storage time, 1999.

	Parameter[y]				
Cultivar	Appearance	Flavor	Sweetness	Tartness	Firmness
'Earlgold'/EMLA7	—[z]	—	—	—	—
'Jonagold'/EMLA111	7.1 a[x]	6.8 a	6.3 a	5.8 b	6.8 a
'Improved Golden'/EMLA7	6.6 a	7.2 a	6.8 a	6.9 a	7.3 a
'Improved Golden'/EMLA111	6.6 a	6.6 a	5.4 b	5.9 b	7.0 a
'Scarlet Gala'/EMLA7	6.9 a	6.5 a	6.1 a	5.8 b	6.6 a
'Jonafree'/Mark	5.3 b	4.5 b	6.5 a	4.0 c	4.5 b
'Macspur'/M7A	5.5 b	5.1 b	4.4 c	4.5 b	4.8 b
'Royal Gala'/MM111	7.3 a	6.7 a	6.5 a	6.2 ab	6.8 a
'Williams Pride'/M7A	—[z]	—	—	—	—

[x]Means in columns separated by Duncan's Mulitple Range Test, $P < 0.05$. Means with the same letter do not differ

[y]Parameters were rated on a 10 point scale, where1 = dislike extremely, and 10 = like extremely

[z]No data presented due to fruit deterioration

Table 4. Maturity indices of apple cultivars measured at harvest time, 1999.

Cultivar	Diameter (cm)	Length (cm)	SSC (°Brix)	pH	Firm (N)
'Earligold'/EMLA7	67.8 b	59.7 bc	12.8 c	3.63 bc	84.8 d
'Jonagold'/EMLA111	75.5 a	63.3 a	13.9 ab	3.6 c	113.7 c
'Improved Golden'/EMLA7	67.4 b	62.5 ab	14.1 a	3.7 b	132.9 bc
'Improved Golden'/EMLA111	63.3 b	56 .8 c	14.1 a	3.7 b	145.5 b
'Scarlet Gala'/EMLA7	64.6 b	58.2 c	13.9 ab	3.75 b	151.2 ab
'Jonafree'/Mark	56.3 c	45.7 d	14.4 a	3.45 d	156.0 a
'Macspur'/MM111	57.5 c	46.2 d	13.4 b	3.4 d	134.3 bc
'Royal Gala'/MM111	65.6 b	59.1 c	13.5 b	3.86 a	133.5 bc
'William's Pride'/M7A	74.1 a	60.3 abc	13.9 ab	3.84 ab	98.5 d

Means separated (by letters) in columns by Duncan's multiple range test, $P > 0.05$

At harvest, consumer preference based on tartness showed that 'Jonagold'/EMLA111, 'Improved Golden'/EMLA7, 'Scarlet Gala'/EMLA7, and 'Royal Gala'/MM111 had the highest rating, while 'Jonafree'/Mark had the lowest rating or least preferred (Table 1). Thirty days after storage, preference based on tartness showed that 'Jonagold'/EMLA111, 'Improved Golden'/EMLA7 'Scarlet Gala'/EMLA7 and 'Royal Gala'/MM111 did not differ. The remaining cultivars were least preferred (Table 2). Sixty days after storage, 'Improved Golden'/EMLA7 were most preferred, followed by the remaining cultivars, except 'Jonafree'/Mark which was least preferred. Tartness ratings for 'Earligold'/EMLA7 and 'William's Pride'/M7A decreased considerably in storage for 60 days and samples were not evaluated due to fruit deterioration.

At harvest, consumer preference based on firmness showed that 'Jonagold'/EMLA111, 'Improved Golden'/EMLA7, 'Improved Golden'/EMLA 111, 'Scarlet Gala'/EMLA7, 'Royal Gala'/MM111 and 'William's Pride'/M7A did not differ and were preferred compared to 'Jonafree'/Mark and 'Macspur'/M7A. 'Earligold'/EMLA7 was the least preferred (Table 3). Thirty days after storage, 'Jona-

gold'/EMLA111, 'Improved Golden'/EMLA7, 'Improved Golden'/EMLA111, 'Scarlet Gala'/EMLA7 and 'Royal Gala'/MM111 were most preferred and did not differ, followed by 'Jonafree'/Mark and 'Macspur'/M7A. 'Earligold'/EMLA7 was least preferred. Sixty days after storage, all cultivars were equally rated, except 'Jonafree'/Mark and 'Macspur'/M7A which were least preferred. 'Earligold'/EMLA7 and 'William's Pride'/M7A were not tested due to fruit deterioration. In Canada, it is assumed that consumers find apples with a firmness of less than 44.5 N too soft (Prange et al., 1993). A sensory evaluation of 'McIntosh' in New York found crispiness to be directly related to firmness. Apples with pressure test values of 85.5 N were rated as "crisp, neither too hard nor too soft" by consumers, while those with firmness of 31.5 to 36 N were rated too soft (Lin and King, 1978).

In general, changes in apple preference with time in storage differed among the cultivar/rootstock combinations tested. Such differences are mainly due to differences in the physiological age of fruit at harvest and losses in fruit quality with time in storage (Wang, 1999).

Relating the sensory evaluation to the analytical data of maturity indices at harvest (Table 4), it was found that the highest preference in appearance coincided with greater fruit length ($r = 0.77$, $n = 24$) and greater fruit diameter ($r = 0.70$, $n = 24$). The least preferred cultivar/rootstock combination, 'Macspur'/M7A, had small fruit. Cultivars intermediate in fruit size, also, maintained a high preference. Factors such as color, fruit shape, and cosmetic appearance were not included in this study, since appearance was based on an overall rating of like or dislike. Such factors must be included considering that most consumers use color as an indicator of ripeness while others look for uniformity of fruit (Brumfield et al., 1993).

Soluble solid content (SSC) and juice pH are commonly used to evaluate fruit flavor. In this study, fruits that had high SSC and high juice pH were not necessarily rated high in flavor, sweetness, and tartness. However, using destructive techniques such as SSC, pH values, and titratable acidity, insures a minimum of quality acceptability for the consumer (Kader, 1999). In comparing firmness at harvest using a penetrometer and firmness by the panelists, it was evident that the more acceptable cultivars by the panelists were firmer at harvest. Two months after harvest, the most preferred cultivars in the sensory test (all the parameters considered) had the highest SSC, juice pH, and firmness values (Table 4). In addition, fruit deterioration of 'Earligold'/EMLA7 and 'William's Pride'/M7A two months after harvest, coincided with the lowest SSC, juice pH, and firmness values of these cultivars which reflected loss of fruit quality due to senescence.

CONCLUSION

In general, this study identified 'Royal Gala'/MM111, 'Jonagold'/EMLA111, 'Improved Golden/EMLA7, 'Improved Golden'/EMLA111, and 'Scarlet Gala'/EMLA7, as the most preferred cultivars both at harvest and after storage. 'Jonafree'/Mark and 'Macspur'/M7A were the least acceptable cultivars for fresh fruit consumption. 'Jonafree' and 'Macspur' are progenies of cultivars traditionally used for baking, therefore, such findings are not surprising. Early harvested cultivars 'Earligold'/EMLA7 and 'William's Pride'/M7A were identified as having poor keeping quality in storage and may be more suitable for the immediate fresh market or short time storage. The consistency in panelists' preference as measured by appearance, flavor, sweetness, tartness, and firmness indicates that such parameters are adequate to determine consumer acceptance.

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Modeling Extinction: Density-Dependent Changes in the Variance of Population Growth Rates

Thomas E. Heering Jr. and David H. Reed[1]
University of Mississippi, Department of Biology, University, MS, 38677-1848

The ability to accurately predict the likelihood of extinction in endangered populations of animals is crucial to many concerns in conservation biology. A number of parameters are generally believed to significantly affect a population's probability of becoming extinct over a given time span. The relationship between the per capita growth rate of a population and its density (i.e., density dependence) is one such parameter. However, the extent to which density dependence influences population dynamics, the usual shape(s) of the density-dependent function, and the impact of density dependence on population persistence, remain controversial. Here we analyze empirical data from 74 populations (40 species) and find evidence for the ubiquity of density dependent population growth. More importantly, using stochastic population models, we find that density-specific changes in the variance of population growth rates have a larger effect on median time until extinction than do changes in the mean population growth rate. Previous studies have focused primarily on density-dependent changes in the mean growth rate. We demonstrate that density-dependent changes in both the mean and the variance of population growth rates can greatly affect the median time to extinction predicted from stochastic population models.

Population growth cannot continue indefinitely in the face of finite resources. As competition for resources increases at higher population densities, the rate of population growth should slow down and eventually stop. Density-dependent population growth is defined as the dependence of the per capita population growth rate on past population densities (Murdoch and Walde, 1989). Ecologists have debated the generality and importance of density-dependent factors (e.g., malnutrition, disease epidemics) to population dynamics for 70 years.

Recent advances in statistical techniques and an increase in the number of long-term ecological studies has led to a growing consensus that density-dependent reproduction and mortality appears to be widespread in natural populations of vertebrates and invertebrates (e.g., Woiwood and Hanski, 1992; Holyoak, 1993; Wolda and Dennis, 1993; Turchin, 1995; Lande et al., 2002), is thought by many to greatly influence the probability of population persistence, and has long been considered important for population dynamics generally (Ferson et al., 1989; Hanski, 1990; Burgman et al., 1993; Dennis and Taper, 1994; Dennis et al., 1995; Hanski et al., 1996; Lande et al., 2002; Sæther et al., 2002; Henle et al., 2004). However, whether density dependence increases or decreases the probability of extinction depends on the exact shape of the density dependent function and its interaction with stochastic factors and life history (Lande et al., 2002; Schoener et al., 2003). For example, the inability of individuals to find a mate or engage in group defense at very low densities might create an absorbing boundary that increases the probability of extinction.

Count-based population viability analyses are often used to estimate population persistence, because these types of data are the ones most often available to conservation biologists (Morris and Doak, 2002). Given a starting population size (N_0), the probability of extinction might simply be determined by the mean (μ) and the variance (σ^2) of the distribution of population growth rates (see Dennis et al., 1991; Reed and Hobbs, 2004).

However, competing claims have been made about the utility and reliability of count-based methods (Brook, 1999; Ludwig, 1999; Fieberg and Ellner, 2000; Meir and Fagan, 2000; Sabo et al., 2004). One potential problem with count-based models is their failure to take into account the dependence of both the mean and the variance of population growth rates on population density. This density-dependence, along with correlation patterns among time points in population size due to the temporal autocorrelation in environmental factors (Pimm and Redfearn 1988; Inchausti and Halley 2001; Reed et al., 2003a), complicates the seemingly simple relationship

[1]Author for correspondence. Department of Biology, P. O. Box 1848; dreed@olemiss.edu

between time until extinction and the mean and variance of population growth rates.

At the heart of this debate is the question of how complex population viability analysis models need to be in order to accurately convey population dynamics. Modeling population dynamics is crucial to determining minimum viable population sizes and ranking conservation priorities. Whether estimates of the density-dependence of population growth rates are necessary for accurate and unbiased estimates of extinction risk is a question of current concern among conservation biologists (e.g., Henle et al., 2004; Sabo et al., 2004).

Despite the importance of the variance in population growth rates, and variance in demographic parameters generally, to all forms of population viability analysis, we are not aware of any published empirical results addressing changes in the variance among population growth rates with changes in density. However, variance in growth rates has been included in a very general way in both diffusion approximations and continuous time Markov chain models of population dynamics (e.g., Mangel and Tier 1993; Wilcox and Elderd, 2003). Here, we examine changes in the variance of population growth rates, as well as changes in the mean growth rate, with density. Further, we demonstrate what effect these changes have on the probability of extinction, as compared to models that disregard density-dependence in population growth rates entirely and to those that only consider changes in the mean population growth rate.

MATERIALS AND METHODS

Stochastic, discrete time, discrete state population models were built from empirical data on the distribution of population growth rates, at different densities, estimated from census data obtained from the Global Population Dynamics Database (GPDD)(NERC 1999) for 74 populations (40 species). The populations used to build the models were chosen based on the following criteria: (1) The quality of the data as determined by the GPDD and the length of the census period assayed. The reliability of the census data is scored by the GPDD from one to five (with five being the most reliable). Data sets were selected for inclusion in the study when the reliability rating multiplied by the census period ≥ 50. (2) The population was judged to be in a stable equilibrium. Thus, the population was not in continuous decline or so far below carrying capacity as to be in a continual growth phase (i.e., the median population growth rate was approximately zero). Extensive analysis of the data sets in the GPDD (Inchausti and Halley, 2001; Reed et al., 2003a,b; Reed, 2004; Reed and Hobbs, 2004) have shown these are the data sets appropriate for answering the questions being addressed in this paper.

Population growth rates (r), for each time step, were calculated using the following formula:

$$r_t = \log_e (N_t / N_{t-1}) \quad (1),$$

where N_t is population size at time t. Positive statistical outliers (especially if they did not seem possible given the species life history) were rare and were removed when detected. However, the distribution of growth rates was normally or approximately normally distributed in all but four cases. Once a distribution of r-values had been calculated the distribution was assayed for evidence of density dependence. Thus, N_{t-1} was regressed against r_t. This regression was allowed to be a first, second, or third order polynomial. We used corrected Akaike Information Criterion statistics (Burnham and Anderson, 2002) and model averaging to identify the best fit model. No time lags were allowed in the density dependence. Solving for the carrying capacity (K) was carried out by setting r_t equal to zero and solving for N. Thus, the carrying capacity is defined as the population size (density) where the mean population growth rate is expected to be zero.

Once values for K were calculated, means and standard deviations for population growth rates were determined for each population at three different density categories: when $N \geq K$ (high density), when $0.5K \leq N < K$ (intermediate density), and when $N < 0.5K$ (low density). Coefficients of variation in the population growth rate (SD_r / r) were also calculated, for each population, at each of the three density categories.

In order to examine the effects of both the mean and the standard deviation of the population growth rate changing with density, we developed a set of stochastic discrete time, discrete state, r-models calibrated from empirical data. The basic format of the model is as follows. First, an initial population size (N_0) was set equal to the initial population size from the actual time series. N_0 was compared to K and a population growth rate (r) randomly chosen from a normal distribution with a mean determined from the regression function and a standard deviation estimated from the actual distribution of growth rates

from the time series. The growth rate is then used to determine population size (N_t) in the next time step. The process is repeated for each time step, with the distribution of possible randomly selected *r* values for each time step being determined by the ratio of *N*:*K* and the regression function. Each model was run for at least 1,000 simulations.

In order to estimate the median time to extinction, we used at least 1,000 simulations of each population. Each simulation had identical starting points and the was allowed to run stochastically for a fixed number of time steps (years). The proportion of replicate populations going extinct within the determined time frame was recorded. The number of time steps was then varied until several estimates of extinction probability above and below 50% were generated. From this data, linear regression was used to estimate the number of time steps sufficient for 50% of the populations to go extinct (median time to extinction). The median time to extinction is certainly not realistic, as no age-structure, explicit demographic stochasticity, or genetic stochasticity was included in the models. However, it still has much heuristic value as concerns the effects of density dependence.

We used corrected Akaike Information Criterion statistics and model averaging (Burnham and Anderson, 2002) to identify what parameters are important with respect to the median time to extinction. Backwards stepwise multiple regression was used to estimate the parameter coefficients from the consensus model. Thirteen variables were initially tested across different model combinations: Initial population size, the carrying capacity (*K*), the median growth rate for the entire census period (r_{med}), the mean growth rate at high densities, the mean growth rate at intermediate densities, and the mean growth rate at low densities, the maximum value of *r* during the census period (r_{max}), the standard deviation in the population growth rate at high densities, the standard deviation in the growth rate at intermediate densities, the standard deviation in the population growth rate at low densities, the coefficient of variation in the growth rate at high densities, the coefficient of variation in the growth rate at intermediate densities, and the coefficient of variation in the population growth rate at low densities. Because standard deviations and coefficients of variation are not independent measures, model selection was based on models that included either the standard deviation or the coefficient of variation, not both. Once the important factors were identified, standardized beta values were calculated to rank the significant factors effects on median time to extinction (Neter et al., 1996).

Sensitivity analysis was performed on the density-specific standard deviation in population growth rates by increasing the standard deviation by 10% increments (up to a maximum increase of 50%) for each density category separately and estimating the slope of the best fit linear line using the standard deviation in the population growth rate as the independent variable and median time to extinction as the dependent variable (Morris and Doak, 2002). The slopes were averaged across all 74 populations and then compared for the three different density categories.

To examine the impact of ignoring density dependence altogether or allowing only the mean growth rate to change, relative to the full model where the mean and variance in growth rates were allowed to change with density, we built additional models for 25 randomly chosen species. Thus, two additional models were constructed with either no density dependence or density dependence where only the mean population growth rate changes with density. Median time to extinction was estimated for models with no density dependence (NDD) and for models where only the mean population growth rate was allowed to change with changing density (SDD). For NDD, the mean population growth rate and the variance among growth rates was the same regardless of density and the values were estimated from the entire census period. For SDD, the variance among growth rates was the same regardless of density, but the mean growth rate changed with density according to the regression function.

We also used an analysis of covariance (using carrying capacity as the covariate) to examine whether there were broad phylogenetic (Class, Order, Family) or environmental (biogeographic region, global latitude) effects on the mean time to extinction.

RESULTS

A meta-analysis of 74 populations was conducted with respect to how the mean, standard deviation, and coefficient of variation in population growth rates changes with changes in population density (Table 1). The mean population growth rate is significantly different at all three density categories and decreases with increasing density across all the 74 populations. Likewise, the standard deviation among

Table 1. Means and standard errors are presented for three different parameters for three different density ranges.

Parameter	Mean ± SE	F	P
CV_r (high)	0.331 ± 0.045	30.57	< 0.0001
CV_r (intermediate)	0.683 ± 0.045		
CV_r (low)	0.205 ± 0.031		
r (high)	-0.155 ± 0.021	123.15	< 0.0001
r (intermediate)	0.082 ± 0.013		
r (low)	0.356 ± 0.035		
SD_r (high)	0.251 ± 0.016	11.29	< 0.0001
SD_r (intermediate)	0.355 ± 0.025		
SD_r (low)	0.515 ± 0.047		

growth rates at a given density significantly decreases with increasing density. The coefficient of variation is also highly significantly different for each density category, but the maximum coefficient of variation is reached at intermediate densities. Thus, density-dependent effects on population growth rate were consistent and highly significant despite the data being noisy (e.g., differences in species biology and generation length, differences in the quality of the data). Further, these density-dependent changes were not just to the mean population growth, but also to two measures of variation in growth rates.

It is important to be able to separate purely demographic causes of variation in growth rates from those brought about by the effects of density. Table 2 provides a comparison between how the standard deviation among population growth rates, for a given density category, changes in large ($K > 200$) versus small ($K \leq 200$) populations. Standard deviations significantly increase with decreasing density in both large and small populations, thus there is an effect of density that is independent of demographic stochasticity. However, the standard deviation is consistently larger in smaller populations, indicating that demographic stochasticity plays a significant role in the amount of variance among population growth rates as well.

We performed model selection using the information-theoretic approach of Burnham and Anderson (2002), using independent combinations of 13 different model parameters (Table 3). The consensus model containing five factors (all significant using multiple regression) are listed and ranked according to their standardized beta values. The significant factors, from greatest effect to least effect are: SD_r (intermediate densities) (F = 23.48, $P < 0.0001$, b = -0.431), K (F = 31.69, $P < 0.0001$, b = 0.398), SD_r (low densities) (F = 9.08, $P < 0.005$, b = -0.242), r (intermediate densities) (F = 8.13, $P < 0.005$, b = 0.196), and r (low densities) (F = 7.52, $P < 0.01$, b = 0.186). The overall regression explains 70.0% of the variation in median extinction times (adjusted R^2= 0.700).

In the Introduction it was suggested that the shape of the density-dependent function for growth rates was important to whether it decreased the probability of extinction (primarily believed to be true) or increased the probability of extinction as might be true with strong Allee effects. We illustrate the five general forms of density dependence in population growth rate found in this study and give their relative frequencies (Figure 1). A linear model was found to be the best fit function for 45 of 74 populations. However, the statistical power to detect nonlinearities in individual data sets was often low. Thus, the lack of evidence for general nonlinearity in the relationship between density and per capita growth rates in these data sets should not be construed as suggesting that such nonlinearities do not exist. A 3rd degree polynomial with population

Table 2. Comparison of the mean (with standard error) standard deviation in population growth rates across the 74 populations, for three different density categories, divided as to whether the carrying capacity was less than or greater than 200 individuals.

	SD_r (N > K)	SD_r (K ≥ N ≥ 0.5K)	SD_r (N < 0.5K)
K ≥ 200	0.18 ± 0.02	0.30 ± 0.04	0.35 ± 0.04
K < 200	0.28 ± 0.02	0.40 ± 0.03	0.58 ± 0.06

growth rates increasing at an increasing rate at very low densities, and decreasing at an increasing rate at very high densities, was the best fit model in 19 of 74 populations. A 2nd degree polynomial where population growth rates increase at an increasing rate at low densities was the best fit in 6 of 74 populations. A 2nd degree polynomial where population growth rates decrease at an increasing rate at both high and low densities was the best fit in 3 of 74 populations. A 2nd degree polynomial where the population growth rate decreases at an increasing rate at high densities was the best fit in only 1 of 74 populations.

An important question in conservation biology is how complex population viability models need to be in order to predict the risk of extinction accurately and without bias. Table 4 shows the results of an analysis of variance comparing median time to extinction, for 25 randomly chosen population models, using three different modeling approaches with the models each developed from the same set of observed data. The models contained either no density dependence, density dependent population growth where the mean growth rate changes with density or population growth rates where the mean and variance were allowed to change with respect to density. The median extinction times for the three models are significantly different from each other ($P < 0.01$), with the models that allow both the mean and variance in population growth rates to change having the longest median times to extinction and those having no density dependence the shortest.

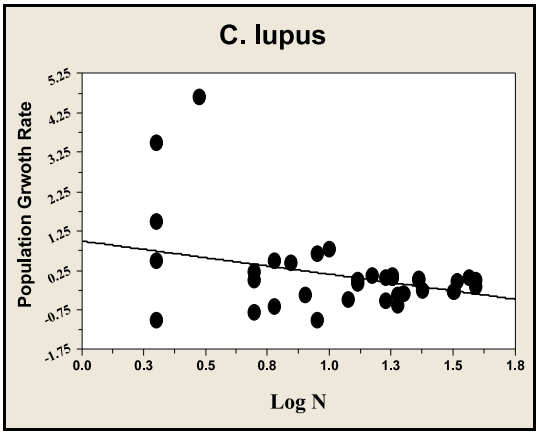
This paper uses the meta-analysis technique to look for factors useful in predicting extinction risk for populations of vertebrates. These techniques are especially important when individual studies cannot be generalized and lack statistical power. However, it is often useful to test for any patterns based on the ecology, life history, or evolutionary histories of the organisms. We find no differences in median time to extinction based on phylogeny (Class, Order, Family) or environmental classification (biogeographic region, global latitude). None of these factors were significant once the effects of carrying capacity were accounted for. These results are congruent with other studies that have looked for these types of effects (Gaillard et al., 2000; Inchausti and Halley, 2001; Reed et al., 2003a; Reed and Hobbs, 2004).

Table 3. The results of multiple regression analysis examining 13 factors suspected of being important in determining median time to extinction in 74 population viability models created from census data on natural populations of animals. The significant parameters from each model are listed in order of importance as determined by their standardized beta values (adjusted $R^2 = 0.700$, $p < 0.0001$).

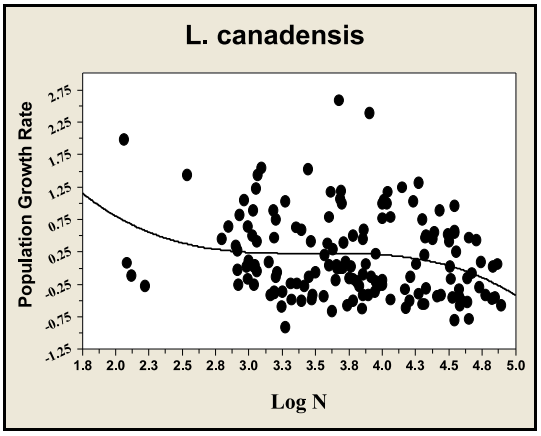
Parameter	Probability	Std Beta
SD_r (medium)	< 0.0001	-0.431
log K	< 0.0001	0.398
SD_r (low)	0.0036	-0.242
r (medium)	0.0036	0.196
r (low)	0.0108	0.186

Table 4. Results from an analysis of variance (randomized block design and Tukey's HSD test), comparing median extinction times (in years) for 25 species. Models were built with either no density dependence (NDD), density dependence where only the mean population growth rate changes with density (DDM), and density dependence where both the mean and standard deviation of the population growth rate were allowed to change with changes in density (DDMS). Each of the three model assumptions leads to significantly different median times to extinction (MT_E) ($F = 18.95$, $p < 0.001$).

Model	MT_E
DDM	476.4
DDMS	913.1
NDD	126.2



A



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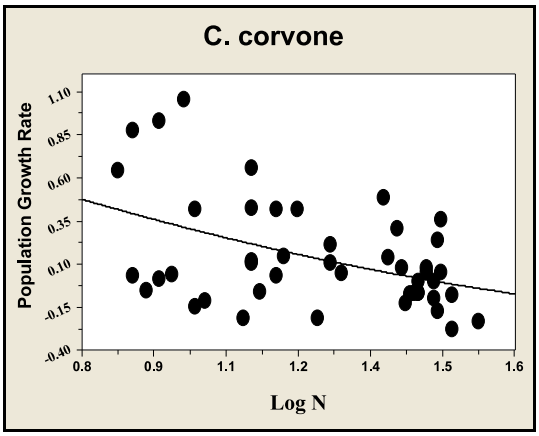

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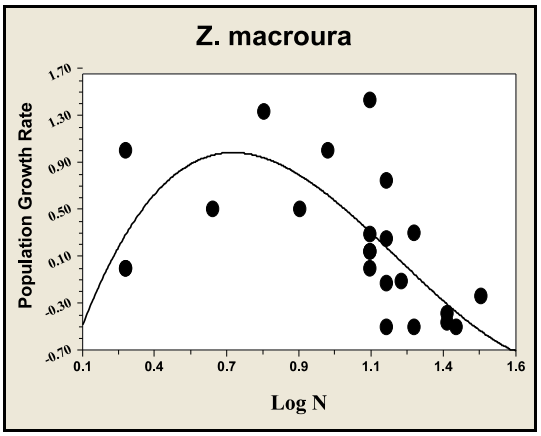

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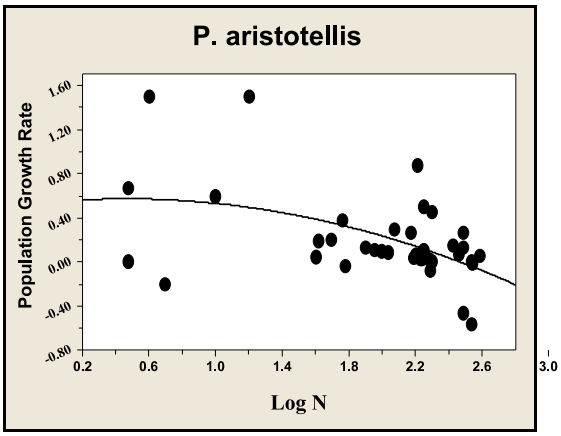

E

Figure 1. Five general forms of density dependence in population growth rate. *(a)* Linear was the best fit function for 45 of 74 populations. Note the decreasing variation in population growth rates with increasing density. *(b)* A 3rd degree polynomial with population growth rates increasing at an increasing rate at low densities, and decreasing at an increasing rate at high densities, was the best fit in 19 of 74 populations. *(c)* a 2nd degree polynomial where population growth rate increases at an increasing rate at low densities was the best fit in 6 of 74 populations. Note the greater variance in growth rates at lower densities. (*d*) a 2nd degree polynomial demonstrating Allee effects was the best fit in 3 of 74 populations. (*e*) a 2nd degree polynomial where population growth rate decreases at an increasing rate at high densities was the best fit in only 1 of 74 populations. Note the greater variance in growth rates at lower densities.

DISCUSSION

Ubiquity of density dependence. The role of density-dependent mortality and birth rates, in impacting population dynamics, has been a source of controversy for at least 70 years (Turchin, 1995). However, there seems to be a growing consensus that most populations (at least at times) are regulated through density-dependent mechanisms in conjunction with stochastic factors (e.g., Turchin, 1995; Sæther et al., 2002; Reed et al., 2003a). There exist far more sophisticated statistical tests for detecting density-dependence than the one we use here (e.g., Dennis and Taper, 1994) and the question of what role density dependence plays in population dynamics will not be answered definitively by this study. However, it is worth noting that the simple regression techniques we used, with an assumption of no time lags and that errors are additive, was significant in 58 of 74 populations examined (78.4%). This is true despite the median time series being only 19 years and the fact that statistical power is reduced if these assumptions are violated (Turchin, 1995). The mean percent of the variance in the per capita population growth rates explained by population size in the previous time step was 29% (SE ± 1.9%) across all 74 populations. Mean population growth rates clearly, consistently, and significantly declined as densities increased. Thus, though not a robust test of the presence of density dependence, this study suggests that density dependence is widespread across vertebrate populations (Appendix I & II).

Density dependent changes in the variance of population growth rates. In addition to changes in the mean per capita population growth rate, changes in the variance among growth rates at different densities were detected. Lower densities led to larger standard deviations among population growth rates. This is expected for demographic reasons alone, because smaller populations are more variable (Taylor et al., 1980; Reed and Hobbs, 2004). Indeed, the data confirm that smaller populations tend to have greater standard deviations at all three density categories (significantly higher at the highest and lowest densities) than do larger populations. However, there are significant changes in the standard deviation among population growth rates with changes in density for the large populations and the same pattern of increasing variance among growth rates with decreasing densities can be seen. Anecdotally, even populations of tens of thousands of individuals still often showed the characteristic increase in the variance among growth rates at lower densities, despite their being so large (even at their lowest observed densities) as to make demographic stochasticity almost nonexistent. Thus, there seems to be a component of the variance among population growth rates that is driven by population densities and not just population size. This suggests, as one possibility, that widespread Allee effects may impact not just the mean but the variance in population growth rates.

Parameters affecting median time to extinction. Five factors were identified as significantly affecting median time to extinction in our models, in rank order of their standardized beta values they are: the standard deviation among population growth rates at intermediate densities, the carrying capacity, the standard deviation among population growth rates at low densities, the mean population growth rate at intermediate densities, and the mean population growth rate at low densities.

It is certainly not surprising to see that carrying capacity is a major factor affecting median time to extinction. Models of population viability are usually sensitive to changes in carrying capacity and there is plenty of empirical data linking larger population size to a greater probability of population persistence (see review in Reed et al., 2003a; O'Grady et al., 2004). The univariate regression gives the following formula for time to extinction at a given carrying capacity:

$$\log_{10} \text{MTE} = 0.9135 + 0.5776 (\log_{10} K) \quad (2),$$

where MTE is the median time to extinction in years and K is the carrying capacity. However, this model undoubtedly overestimates median time to extinction. In fact, these stochastic r models predict median extinction times that are more than five times as long (K = 10), three times as long (K = 100), or 1.5 times as long (K = 10,000) as models that incorporate far greater complexity (Reed et al., 2004).

The standard deviation in the population growth rate is more important than the mean of the population growth rate, in determining median time to extinction. Thus, models that are deterministic or do not carefully consider estimates of the variation in population growth rates, or demographic parameters generally, will not be able to provide accurate information on the probability of extinction.

The median time to extinction was most affected by both the standard deviation in population growth rates and the mean population growth rate at interme-

diate densities. This is contrary to intuition, as it might be expected that populations would be most vulnerable to extinction when they are at their lowest densities (smallest size). It is possible that this result is simply due to there being so much more variation among models for the parameters at this density. With this hypothesis in mind, we conducted sensitivity analysis on changes in the standard deviation among growth rates for all three densities for 30 randomly chosen models. Using multiple regression, we found that the models were most sensitive to changes in the standard deviation at the lowest densities (data not shown) as expected from theory. The differences in sensitivity at low and intermediate densities was small, but statistically significant.

Importance of including density-dependent changes in the mean and variance. We are not the first to suggest that density dependence is an important component to include in population viability models (see Introduction). In our simple count-based population viability analysis for 25 species, the median time to extinction without density dependence was less than 30% of the median time to extinction when density dependence was included. Thus, the models without density dependence were not just pessimistic, but they were extremely pessimistic relative to the models with density dependence. This suggests that density dependence generally "puts the brakes on" declining populations by creating reflecting rather than absorbing points at low densities.

Including changes in the variance among population growth rates, in addition to changes in the mean growth rate, nearly doubles persistence time over the case where only the mean growth rate is allowed to change with density. This seems counterintuitive at first, given that the variance among growth rates increases as population sizes decline and this is precisely when populations are most vulnerable. However, the reason for this is that the density-specific variance, even at low densities, is less than the variance among population growth rates for the entire census period. Thus, extreme caution must be used in building count-based PVAs from census data even in equilibrium populations. Simply computing the mean and variance of the growth rates over a given number of time steps is not likely to produce the type of dynamics and, therefore, extinction probabilities that exist in natural populations. The reasons why this is true include the autocorrelation structure in environmental variation through time (Pimm and Redfearn, 1988; Reed et al., 2003a), the lack of inclusion of rare catastrophic events that greatly impact population persistence (Reed et al., 2003b), and density dependent changes in the mean and variance of population growth rates.

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Appendix I: Class, order, and biogeographic zone for each of the 40 species modeled.

Species	Class	Order	Biogeographic Zone
Vanellus vanellus	Aves	Charadriiformes	Palaearctic
Rissa tridactyla	Aves	Charadriiformes	Nearctic
Zenaida macroura	Aves	Columbiformes	Nearctic
Accipiter nisus	Aves	Falconiformes	Palaearctic
Falco rusticolus	Aves	Falconiformes	Nearctic
Alauda arvensis	Aves	Passeriformes	Palaearctic
Corvus corone	Aves	Passeriformes	Palaearctic
Corvus frugilegus	Aves	Passeriformes	Palaearctic
Cyanocitta cristata	Aves	Passeriformes	Palaearctic
Melospiza melodia	Aves	Passeriformes	Nearctic
Spizella pusilla	Aves	Passeriformes	Nearctic
Fringella coelebs	Aves	Passeriformes	Palaearctic
Fringella montifringella	Aves	Passeriformes	Palaearctic
Anthus pratensis	Aves	Passeriformes	Palaearctic
Ficedula albicollis	Aves	Passeriformes	Palaearctic
Ficedula hypoleuca	Aves	Passeriformes	Palaearctic
Parus atricapillus	Aves	Passeriformes	Nearctic
Parus bicolor	Aves	Passeriformes	Nearctic
Parus caeruleus	Aves	Passeriformes	Palaearctic
Parus major	Aves	Passeriformes	Palaearctic
Sturnus vulgaris	Aves	Passeriformes	Palaearctic
Phylloscopa collybita	Aves	Passeriformes	Palaearctic
Phylloscopa trochilus	Aves	Passeriformes	Palaearctic
Phalacrocorax aristotellis	Aves	Pelecaniformes	Palaearctic
Picoides pubescens	Aves	Piciformes	Nearctic
Ovis canadensis	Mammalia	Artiodactyla	Nearctic
Tragelaphus strepsiceros	Mammalia	Artiodactyla	Ethiopian
Dama dama	Mammalia	Artiodactyla	Palaearctic
Canis lupus	Mammalia	Carnivora	Palaearctic
Lynx canadensis	Mammalia	Carnivora	Nearctic
Enhydra lutris	Mammalia	Carnivora	Nearctic
Gulo gulo	Mammalia	Carnivora	Nearctic
Martes americana	Mammalia	Carnivora	Nearctic
Phoca groenlandica	Mammalia	Carnivora	Nearctic
Phoca vitulina	Mammalia	Carnivora	Palaearctic
Ursus arctos horribilis	Mammalia	Carnivora	Nearctic
Microtus californicus	Mammalia	Rodentia	Nearctic
Merlangus merlangius	Osteichthyes	Gadiformes	Palaearctic
Perca fluviatalis	Osteichthyes	Perciformes	Palaearctic
Esox lucius	Osteichthyes	Salmoniformes	Palaearctic

Appendix II: F(x) = shape of density dependent function (see Figure 1), r^2 = proportion of variance in the population growth rate explained by density in the preceding time step, MT_E = median time to extinction, K = carrying capacity, r (K_n) = the mean population growth rate at high, intermediate and low densities (K_1, K_2, and K_3, respectively), and SD_r (K_n) = the standard deviation among population growth rates at high, intermediate, and low densities (K_1, K_2, and K_3, respectively).

Species	$F_{(x)}$	r^2	MT_E	K	r (K_1)	r (K_2)	r (K_3)	SD_r (K_1)	SD_r (K_2)	SD_r (K_3)
Vanellus vanellus	a	0.06	8	13	-0.033	0.078	0.143	0.382	0.496	0.685
Vanellus vanellus	a	0.12	33	19	-0.249	0.151	0.339	0.287	0.292	0.659
Rissa tridactyla	b	0.39	919	171	-0.040	0.069	0.181	0.120	0.112	0.198
Zenaida macroura	d	0.45	33	24	-0.395	0.172	0.619	0.117	0.527	0.516
Zenaida macroura	a	0.34	21	110	-0.147	0.146	0.321	0.516	0.415	0.214
Accipiter nisus	a	0.08	329	111	-0.055	0.027	0.033	0.077	0.197	0.047
Accipiter nisus	a	0.87	710	52	-0.058	0.223	1.035	0.093	0.055	2.309
Falco rusticolus	b	0.20	144	82	-0.041	0.007	0.297	0.308	0.323	0.488
Alauda arvensis	c	0.48	213	57	-0.043	0.095	0.353	0.124	0.223	0.719
Corvus corone	c	0.44	181	17	-0.109	-0.020	0.139	0.160	0.231	0.266
Corvus frugilegus	a	0.24	58	355	-0.073	-0.044	0.051	0.075	0.214	0.249
Corvus frugilegus	a	0.54	315	126	-0.121	-0.049	0.249	0.174	0.179	0.234
Cyanocitta cristata	a	0.24	246	26	-0.090	0.073	0.252	0.206	0.267	0.372
Melospiza melodia	a	0.57	26	52	-0.200	0.281	0.568	0.417	0.365	0.096
Spizella pusilla	b	0.29	273	65	-0.107	0.031	0.185	0.326	0.332	0.287
Fringella coelebs	a	0.09	1581	616	-0.028	0.016	0.047	0.100	0.062	0.147
Fringella montifringilla	a	0.19	55	71	-0.109	-0.030	0.365	0.399	0.371	0.463
Anthus pratensis	a	0.34	252	88	-0.096	0.017	0.079	0.123	0.142	0.301
Ficedula albicollis	a	0.36	9	8	-0.139	0.034	1.206	0.440	0.335	1.706
Ficedula albicollis	a	0.03	834	99	-0.131	0.042	0.184	0.184	0.214	0.060
Ficedula hypoleuca	a	0.28	10	9	-0.238	0.188	0.495	0.302	0.619	0.746
Ficedula hypoleuca	d	0.87	444	82	-0.092	0.184	0.758	0.133	0.269	0.719
Ficedula hypoleuca	c	0.23	551	144	-0.046	-0.022	0.141	0.117	0.154	0.146
Parus atricapillus	b	0.58	498	114	-0.158	0.340	0.525	0.257	0.387	0.526
Parus bicolor	a	0.32	16	8	-0.237	0.067	0.625	0.275	0.458	0.744
Parus bicolor	d	0.10	5	12	-0.294	-0.141	0.116	0.131	0.516	0.729
Parus bicolor	a	0.37	7	17	-0.210	-0.015	1.333	0.347	0.666	1.282
Parus caeruleus	b	0.46	46	46	-0.075	0.113	0.359	0.284	0.479	0.535
Parus caeruleus	a	0.55	96	82	-0.193	0.136	0.378	0.203	0.451	0.365
Parus caeruleus	a	0.25	745	74	-0.067	0.085	0.436	0.228	0.345	0.302
Parus caeruleus	b	0.35	81	89	-0.169	0.168	0.259	0.300	0.333	0.517
Parus caeruleus	a	0.24	53	44	-0.122	0.098	0.367	0.193	0.389	0.621
Parus caeruleus	b	0.22	151	87	0.037	0.027	0.199	0.399	0.290	0.254
Perca fluviatalis	a	0.41	9	18	-0.037	0.031	0.481	0.210	0.211	0.105
Perca fluviatalis	a	0.14	41	180	-0.184	0.127	0.261	0.294	0.675	0.145

Appendix II: Cont'd.

Species	$F_{(x)}$	r^2	MT_E	K	r (K_1)	r (K_2)	r (K_3)	SD_r (K_1)	SD_r (K_2)	SD_r (K_3)
Parus major	a	0.45	131	126	-0.307	0.353	0.709	0.254	0.469	0.387
Parus major	a	0.41	293	208	-0.246	0.092	0.366	0.090	0.372	0.295
Parus major	a	0.25	103	27	-0.087	-0.065	0.282	0.249	0.158	0.495
Parus major	b	0.21	468	94	-0.015	0.038	0.329	0.154	0.230	0.405
Sturnus vulgaris	c	0.27	188	54	-0.026	0.103	0.222	0.188	0.395	0.431
Sturnus vulgaris	b	0.19	41	62	-0.140	0.241	0.402	0.434	0.500	0.685
Sturnus vulgaris	a	0.35	356	61	-0.269	0.032	0.268	0.189	0.233	0.280
Phylloscopa collybita	a	0.37	92	12	-0.210	0.091	0.469	0.248	0.288	0.460
Phylloscopa trochilus	b	0.45	5	7	-0.441	-0.032	0.500	0.498	0.302	1.389
Phylloscopa trochilus	a	0.13	17	9	-0.059	0.038	0.260	0.333	0.461	0.522
Phalacrocorax aristotellis	e	0.22	1258	399	-0.019	0.002	0.286	0.046	0.326	0.433
Picoides pubescens	a	0.33	54	5	-0.098	-0.052	0.597	0.494	0.269	0.392
Picoides pubescens	a	0.16	39	8	-0.080	0.056	0.348	0.273	0.423	0.429
Ovis canadensis	b	0.21	1192	185	-0.033	0.039	0.199	0.235	0.273	0.375
Tragelaphus strepsiceros	a	0.06	92	6327	-0.086	0.003	0.027	0.097	0.153	0.191
Tragelaphus strepsiceros	a	0.46	1387	58502	-0.045	-0.006	0.260	0.147	0.098	0.405
Dama dama	a	0.38	1987	970	-0.028	-0.015	0.091	0.088	0.074	0.065
Canis lupus	a	0.14	44	399	-0.106	0.246	0.193	0.322	0.526	0.499
Lynx canadensis	c	0.20	342	3598	-0.072	0.111	0.355	0.264	0.386	0.594
Lynx canadensis	a	0.19	1557	31915	-0.074	0.044	0.462	0.207	0.507	0.805
Lynx canadensis	b	0.05	1261	42300	-0.186	0.081	0.235	0.257	0.172	0.353
Enhydra lutris	a	0.22	1563	1753	-0.096	0.080	0.072	0.199	0.195	0.170
Gulo gulo	b	0.05	417	682	-0.033	0.032	0.056	0.138	0.184	0.308
Gulo gulo	b	0.07	1692	799	-0.139	0.041	0.176	0.167	0.151	0.399
Martes americana	a	0.26	15	73	-0.136	-0.095	0.625	0.558	0.227	0.873
Martes americana	a	0.12	552	44958	-0.117	0.136	0.158	0.264	0.367	0.315
Martes americana	a	0.29	779	168	-0.130	0.152	0.279	0.158	0.277	0.202
Phoca groenlandica	c	0.42	108	96	-0.230	0.225	0.756	0.157	0.475	0.076
Phoca vitulina	b	0.38	2368	1537	-0.001	0.006	0.061	0.067	0.071	0.257
Phoca vitulina	b	0.56	843	1208	-0.772	0.058	0.070	0.097	0.104	0.061
Phoca vitulina	b	0.27	538	135	-0.089	-0.034	0.002	0.122	0.137	0.075
Ursus arctos horribilis	a	0.26	1352	81	-0.052	0.007	0.083	0.189	0.078	0.264
Microtus californicus	a	0.11	3	54	-0.530	0.300	1.070	0.396	1.246	2.099
Microtus californicus	b	0.14	11	311	-0.044	0.200	0.317	0.214	0.702	0.848
Merlangus merlangius	a	0.30	211	1619	-0.432	0.497	0.324	0.237	0.613	0.222
Esox lucius	a	0.33	349	1967	-0.136	0.046	0.046	0.209	0.244	0.154
Esox lucius	a	0.19	221	2895	-0.044	-0.038	0.336	0.216	0.287	0.643

New Records for the Phlebotomine Sand Fly *Lutzomyia shannoni* (Dyar) (Diptera: Psychodidae) in Mississippi

Jerome Goddard[1] and Chad P. McHugh

Mississippi Department of Health, Jackson, MS 39215, and
Air Force Institute for Operational Health, Brooks City-Base, TX 78235

Phlebotomine sand flies are delicate, hairy, mosquito-like insects occurring mainly in the tropics and subtropics. They are notorious vectors of agents of several deadly and disfiguring diseases such as Leishmaniasis, sand fly fever, and bartonellosis (Lane 1996). *Lutzomyia shannoni* (Dyar) is one of the more thoroughly studied species of the phlebotomine sand flies in North America (Figure 1). The various life stages were figured by Hanson (1968) and Young and Perkins (1984). Brinson et al. (1992) and Comer et al. (1994b) documented the seasonal abundance of adults in Georgia. The former authors also documented the vertical distribution of adults, while the latter determined there were three generations per year. Hosts for the blood-feeding females include white-tailed deer, feral swine, donkeys, horses, raccoons (Comer et al. 1994a), and humans (Thurman et al. 1949, Snow 1955). Ecologically, *Lu. shannoni* is associated with live oak (*Quercus viginiana* Miller) forests and, to a lesser extent, mixed hardwood forests where an abundance of tree holes provides diurnal resting sites for adults (Comer et al. 1993).

In the eastern United States, *Lu. shannoni* is a vector of vesicular stomatitis virus (Corn et al. 1990, Comer et al. 1994b) and, because females transmit the virus transovarially to a percentage of their progeny (Comer et al. 1990), the species provides an overwintering mechanism for the virus. Lawyer and Young (1987) determined *Lu. shannoni* also is a competent vector of *Leishmania mexicana* (Biagi), a parasitic protozoan that may be enzootic in the southeastern United States (McHugh et al. 2003), and unidentified flagellates were detected in *Lu. shannoni* collected in Florida (Perkins 1982).

Lutzomyia shannoni has a discontinuous range from Argentina to the United States with a gap in Texas and northern Mexico, possibly due to the absence of extensive hardwood forests (Young and Duncan 1994). In the United States, it occurs in the southeastern states from Louisiana and Arkansas to Maryland and Delaware. However, collection records in this country are spotty, and the species has been reported in only 45 counties. In Mississippi, it previously was known from only two counties. Young and Perkins (1984) reported the collection of two males and 37 females by V. Newhouse in Hancock County, and Rozeboom (1944) identified an unknown number of *Lu. shannoni* from Clinton, Hinds County, in the collection of the U.S. National Museum. A search for phlebotomines revealed no specimens in either the Mississippi Entomological Museum at Mississippi State University (R. Brown, pers. comm.) or the insect collection at the University of Mississippi (P. K. Lago, pers. comm.). In this note, we report additional collection records for *Lu. shannoni* in Mississippi, including three new county records (dates preceded by an asterisk).

Centers for Disease Control miniature light traps supplemented with dry ice were used for all collections. Traps were set in areas of mature, mixed oak-

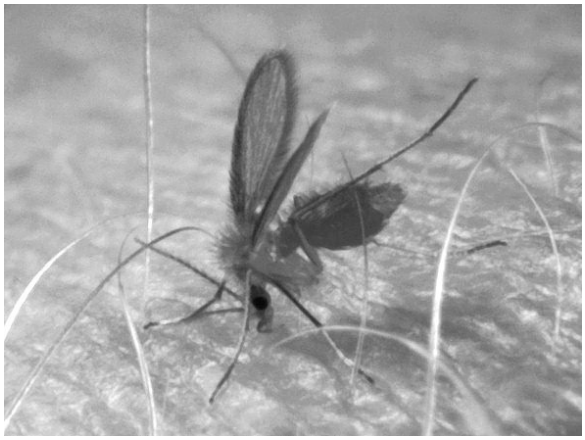

Figure 1. Adult sand fly feeding (Photo courtesy the U.S. Armed Forces Pest Management Board, photo by Dr. Edgar Rowton).

[1]Author for correspondence. Mississippi Department of Health, P.O. Box 1700, Jackson, MS 39215. Telephone 601-576-7689.

hickory-pine forests containing predominantly hardwoods such as red oak, chestnut oak, white oak, sweet gum, sycamore, various hickory species, and loblolly pine. A large number of the hardwoods contained tree holes. Specimens were identified using the key of Young and Perkins (1984), and voucher specimens were deposited with the Mississippi Entomological Museum at Mississippi State University, Starkville, Mississippi.

County records: COPIAH: *2-V-2001, Copiah County Game Management Area (GMA), J. Goddard, 2 females. 15-XI-2001, Copiah GMA, J. Goddard, 2 females. 21-IX-2004, Copiah GMA, J. Goddard, 1 female. 30-IX-2004, Copiah GMA, W. Varnado, 1 female, 1 male. 1-X-2004, Copiah GMA, W. Varnado, 1 female, 2 males. HINDS: 15-VIII-2003, Byram, J. Goddard, 1 female. 6-V-2004, Byram, J. Goddard, 1 male. LEAKE: *16-IX-2004, near Carthage, J. Goddard, 1 female. TISHOMINGO: *1-VI-2004, Tishomingo State Park, J. Goddard, 1 female. 4-VI-2004, Tishomingo State Park, W. Varnado, 19 females, 8 males.

Although these records more than double the known collections in Mississippi, our knowledge of the distribution of *Lu. shannoni* is still incomplete. The paucity of records for *Lu. shannoni* specifically, and phlebotomines generally, reflects the scarcity of workers intentionally targeting sand flies for collection. Thus, at the present time, the known distributions of this and other phlebotomine species represent more the distribution of collectors than that of the sand flies themselves.

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President's Column

As my term as President of the Mississippi Academy of Sciences draws to a close, I would like to thank the Members of the Academy and the Board of Directors for the opportunity to serve the Academy. It has, truly, been an honor and a pleasure. This year has been exceptionally active and, I believe, successful. The annual meeting was held at a new venue, which met with an overwhelmingly positive response. The processes of planning and preparing for the annual meeting were the result of many hours of diligent work by a large number of persons, as mentioned in my most recent President's column. What was remarkable to me was the team effort that occurred to make the meeting run smoothly; I remain amazed at the dedication of our members. In addition to a successful annual meeting, and thanks to dedicated editorial leadership, the MAS Journal has continued publish quality scholarly works and rivals the journals published by many of the Academies of Science of much larger States. I applaud the editorial board for their efforts, and look forward to continued success.

Of the many persons who assisted me throughout the year, the efforts of Ms. Cynthia Huff in the MAS office were invaluable. It has been her guidance and assistance throughout the entire year that made the year successful, and will help guide the transition to our new President, Dr. Larry McDaniel. I look forward to another successful year for MAS under his leadership. Thank you, again, for the opportunity to serve as President of the Mississippi Academy of Sciences.—Sarah Lea McGuire