

Chapter 7

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Hatching asynchrony in parrots: Boon or bane for sustainable use?

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Recently biologists have become increasingly alarmed over the accelerating loss of biodiversity, particularly in tropical regions. Academic scientists, including most behaviorists, are now trying more than ever to apply their seemingly irrelevant knowledge and expertise to real world conservation problems.

Among a broad range of strategies proposed to conserve biodiversity (Soulé 1991) is a growing interest in the pragmatic approach that stresses the value of maintaining healthy ecosystems and populations. Conservation efforts may be most effective when organisms and ecosystems 'pay their own way,' either through the value of the goods and services provided by an ecosystem, or by utilizing particular organisms with economic value in a sustainable manner (e.g., Fearnside 1989; Robinson & Redford 1991a; Balick & Mendelsohn 1992). Sustainable use is one conservation strategy where the need for basic behavioral and ecological research has been particularly recognized (Lubchenco *et al.* 1991; Mangel *et al.* 1993; Meyer & Helfman 1993).

In many cases a behaviorist's evolutionary perspective, using multiple working hypotheses, can provide unique insights into effective management options (Arcese *et al.*, Chapter 3). We present a case study showing how theory-based behavioral studies can be not only useful, but essential, for developing appropriate and effective conservation strategies. Specifically, we discuss how studies of incubation behavior in parrots can provide useful information for the design and implementation of sustainable harvest programs. Many parrots in the world are highly valued in the international pet trade, so a program of sustainable harvest may be a feasible conservation option for them (Thomsen & Brautigam 1991; Beissinger & Bucher 1992a). Unfortunately, knowledge of the basic biology of these birds lags behind the need for such information to

establish sustainable levels of harvest and to increase the productivity of managed populations. Studies of parrot behavior can help to bridge that gap.

The current conservation crisis of parrots

Status of parrot populations

Parrots (family Psittacidae) are one of the most threatened groups of birds in the world (Beissinger & Snyder 1992). Approximately one-third of the 140 New World species of macaws, parrots, and parakeets are considered to be at risk of extinction (Collar & Juniper 1992). These threatened species are concentrated in relatively small areas of the Neotropics, primarily in the Andean highlands, Atlantic forests of Brazil, and islands of the Caribbean (Collar & Juniper 1992). With few exceptions, populations of almost all New World parrot species are thought to be declining (Collar & Juniper 1992).

The status of Old World parrots is much less comprehensively known. In Australia many forest species are known to be endangered or declining, although several non-forest species have increased dramatically with the expansion of industrialized agriculture (Long 1984; Joseph 1988). Relatively few parrots of Africa or mainland Asia are currently considered endangered, but this may reflect a lack of information more than healthy population levels (Collar & Stuart 1985; Collar *et al.* 1994). A high proportion of species inhabiting islands are threatened or declining, in part because many occupy very restricted ranges (e.g., Lambert 1985; Taylor 1985; Merritt *et al.* 1986; Rinke 1989; Evans 1991; Robinet *et al.* 1995).

Causes for declines in parrot populations

Parrot populations are declining for two primary reasons: habitat destruction and direct exploitation for the wild bird trade (Fig. 7.1). As with most threatened organisms, habitat destruction is an important factor reducing population sizes for many parrot species. Tropical habitats, particularly forests, are being destroyed through logging, conversion to agriculture, and urbanization. Burgeoning human populations and problems of poverty and inadequate land tenure have accelerated these losses. Parrot species inhabiting montane forests have been especially hard hit because highland regions in the tropics are the most favored areas for

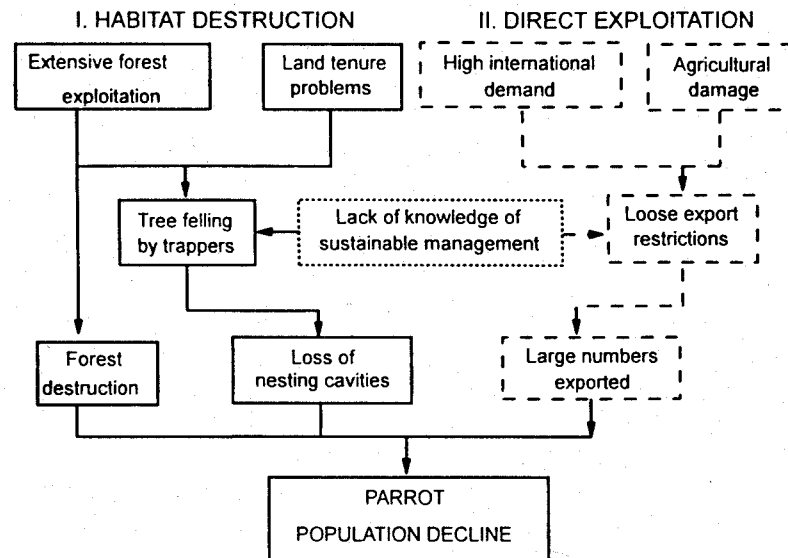


Fig. 7.1. Two separate paths have caused drastic population declines of Neotropical parrots: habitat destruction and direct exploitation for the pet trade. Providing the information needed for sustainable management potentially addresses both paths. Adapted from Beissinger & Bucher (1992a).

settlement and agriculture (Houghton *et al.* 1991). Habitat loss is thought to be wholly or partially responsible for population declines in over two-thirds of all parrot species (Collar & Stuart 1985; Collar & Juniper 1992). In Australia, where the capture and exportation of wild parrots was banned in the 1950s, habitat loss resulting from agricultural practices is the single most important cause of population declines (Joseph 1988; Joseph *et al.* 1991; Saunders 1991).

Outside of Australia, parrots bear the additional burden of being exploited directly for the pet trade. Large numbers of wild caught birds are transported from developing tropical countries to developed countries each year. Over 250 000 psittacines were exported annually from mainland Neotropical countries between 1982 and 1986 (Thomsen & Brautigam 1991). The impact of harvesting on wild populations is greater than export figures suggest because pre-export mortality may exceed 50% of individuals captured (Iñigo-Elias & Ramos 1991). In most countries the volume of non-export, internal trade is also high (Beehler 1985; Desenne & Strahl 1991; Thomsen & Brautigam 1991). Exploitation

for the pet trade affects over half of all parrot species (Smiet 1985; Jorgenson & Thomsen 1987; Thomsen & Mulliken 1992).

Additional factors are a major cause of mortality in some psittacine populations. Island populations have been hard hit by introduced predators (e.g., Beggs & Wilson 1991; Gnam & Rockwell 1991; Robinet *et al.* 1995). Hunting of parrots for food or plumes by indigenous peoples can be a significant source of mortality in remote areas (Beehler 1985; Redford & Robinson 1987).

The two processes of habitat loss and direct exploitation represent two distinct avenues for population declines in parrots (Fig. 7.1; Beissinger & Bucher 1992a). Conservation solutions that address one suite of problems fail to affect the other. For example, while habitat protection may be necessary for supporting parrot populations, it is insufficient as long as economic incentives for capturing wild birds exist. On the other hand, an import ban to reduce the demand for wild birds would do nothing to alleviate the rate of forest destruction in the tropics (Beissinger & Bucher 1992a).

Life history and behavior of parrots

The decline of parrot populations from habitat loss and direct exploitation is exacerbated by certain characteristics of the life history and behavior of parrots. Parrots have low reproductive rates because of slow maturation, small clutch sizes in larger species, and a high proportion of non-breeders (e.g., Lanning & Shiflett 1983; Smith & Saunders 1986; Gnam & Rockwell 1991; Munn 1992; Navarro *et al.* 1992). In most populations only a small proportion of potential breeders actually attempt to breed in any given year. For example, in the Puerto Rican parrot (*Amazona vitatta*), non-breeders comprise 57% of the population (Snyder *et al.* 1987). In the Manú Biosphere Reserve, Perú, only 10 to 20% of adult mated pairs of macaws (*Ara spp.*) nest in any given year (Munn 1992). In our own studies of the Green-rumped parrotlet (*Forpus passerinus*), an average of 37% of the banded adults seen did not breed in any given year (unpublished data). This figure certainly underestimates the actual proportion of non-breeders in our study population because our banding and resighting efforts have focused on breeding birds. The net result of having a large proportion of non-breeders is that the effective size of any parrot population is actually much smaller than its census size. Also, parrots exhibit asynchronous hatching, which frequently results in the mortality of the smallest young (Rowley 1990; Beissinger & Waltman 1991).

Almost all species are secondary cavity nesters, and therefore nest sites may be limited (Snyder 1977; Forshaw 1989). In many species of hole-nesting birds, the size of the breeding population is constrained by the availability of nest sites (Newton 1994). Local people frequently destroy nesting trees to gain access to nestlings for the pet trade. This activity compounds the loss of nest sites because of habitat destruction.

Conservation alternatives for parrots

Three general conservation strategies based on biological factors have been suggested as appropriate for parrots (Beissinger & Snyder 1992): habitat protection, captive breeding, and sustainable harvesting for the pet trade.

Habitat protection

Habitat protection is crucial for maintaining any wild population. Protecting essential habitat for parrots has the advantage of protecting other organisms that share the habitat. Many parrot species, however, do not require pristine habitat, and can thrive in disturbed areas (e.g., Snyder *et al.* 1987; Bucher 1992; Waltman & Beissinger 1992; Wiley *et al.* 1992). More importantly, habitat protection alone does not address the problem of direct exploitation (Redford 1992). Thus, habitat protection is necessary but not sufficient for conserving many parrot species.

Captive breeding

Ideally captive breeding programs could provide parrots for reintroductions or to augment existing populations; however, many problems interfere with its implementation and use (Derrickson & Snyder 1992; Wiley *et al.* 1992). To start a captive population, individuals must be removed from the wild, exacerbating the problems inherent in small populations. Captive breeding programs are very expensive compared with *in situ* methods; channeling scarce funds into captive breeding may pre-empt more cost-effective *in situ* techniques (Snyder *et al.* 1996). Once implemented, captive breeding programs for parrots face numerous and significant problems, including obtaining consistent reproduction, avoiding progressive domestication, controlling disease, reintroducing

captive-raised birds into the wild, and maintaining financial and administrative support (Dobson & May 1986; Derrickson & Snyder 1992).

Captive breeding for the purpose of conserving threatened parrots has had little success in the past and is unlikely to prove successful at rescuing wild populations of parrots in the future. Captive programs ignore the ultimate causes of population declines in parrots: habitat loss and exploitation for the bird trade. Captive breeding, therefore, is not a useful tool for parrot conservation, except in a few extreme cases in which a species is in imminent danger of extinction, such as the Puerto Rican parrot or Spix's macaw (Snyder *et al.* 1987; Juniper & Yamashita 1991). Aviculturalists have argued that captive breeding may help to alleviate the pressures on wild populations by supplying birds for the pet trade. The costs of captive production far exceed the costs of harvesting and transporting wild birds, however (Chubb 1992). Captive-bred birds are unlikely to compete successfully in the marketplace as long as there are wild birds to be caught (Thomsen & Brautigam 1991; Derrickson & Snyder 1992).

Sustainable harvesting

Proponents have promoted sustainable use as a way to integrate conservation priorities with social and economic necessities (Reid 1989; Lubchenco *et al.* 1991), although the definition and even the attainability of sustainable use are debated (Simon 1989; Ludwig *et al.* 1993; Mangel *et al.* 1993). Here we use the following definition: sustainable harvesting refers to the continued persistence and replenishment of a resource despite utilization (Beissinger & Bucher 1992a). The conservation function of sustainable harvesting of parrots is to provide the pet trade with an abundant, dependable source of birds, while simultaneously providing local people with economic incentives to maintain healthy populations of parrots and their habitats. Thus, sustainable utilization of parrots may address both of the ultimate causes of declining parrot populations (Fig. 7.1).

Before sustainable harvesting programs can be implemented, substantial information is required about population structure, factors that limit reproduction, and habitat requirements (Beissinger & Bucher 1992a,b). Long-term studies with marked individuals are required to collect this information. Once determined, factors that limit populations may be manipulated to increase the productivity of a population.

Models for sustainable harvesting

In a sustained yield model, the harvest rate used is the annual increment to the population such that the net change in the population size after harvesting is zero. Typically, the harvest levels used are near the maximum sustained yield, which is that level of harvest from the population size where the population growth rate is maximized. In traditional natural resource management of timber or fisheries, the maximum sustained yield is usually achieved when populations are at about half of their carrying capacity, assuming a logistic growth pattern for the population (Fig. 7.2a).

Traditional maximum sustained yield models are not really appropriate for parrots because often the models do not differentiate between individuals of different age classes. Most managed species are harvested as adults. With parrots, however, nestlings are preferable to adults for harvesting because: (1) chicks make better pets than wild-caught adults; (2) chicks bring higher market prices than adults; and (3) chicks have a lower reproductive value to the population than adults (Fisher 1930). If only nestlings are to be harvested, then the harvestable portion of the population is maximized when the population is near its carrying capacity (Fig. 7.2b). Logically, the more birds there are in the population, the more harvestable young they can produce. Thus, a program of sustainable harvesting of parrots would not only reduce pressure from the pet trade on wild populations, but also provide incentives to maintain robust population sizes.

In species such as parrots where we lack sufficient biological knowledge to establish sustainable harvest rates, the use of a Conservative Sustained Harvest model is warranted (Beissinger & Bucher 1992a,b). This approach suggests that when a population is increasing or stable, then any management programs that increase productivity would lead to a harvestable surplus (Fig. 7.3). By managing factors that limit population growth, productivity may be increased by: (1) increasing the number of breeders within the population; (2) increasing the proportion of breeders that successfully fledge young; or (3) increasing the number of young fledged per successful nest (Beissinger & Bucher 1992a,b). The number of breeders in a population may be increased by providing supplemental food or nest sites (boxes). The proportion of successful breeders can be increased by adding or predator-proofing nest boxes. Fledging success may be improved by adding nest boxes (to decrease the incidence of infanticide), providing supplemental food, or forcing double clutching

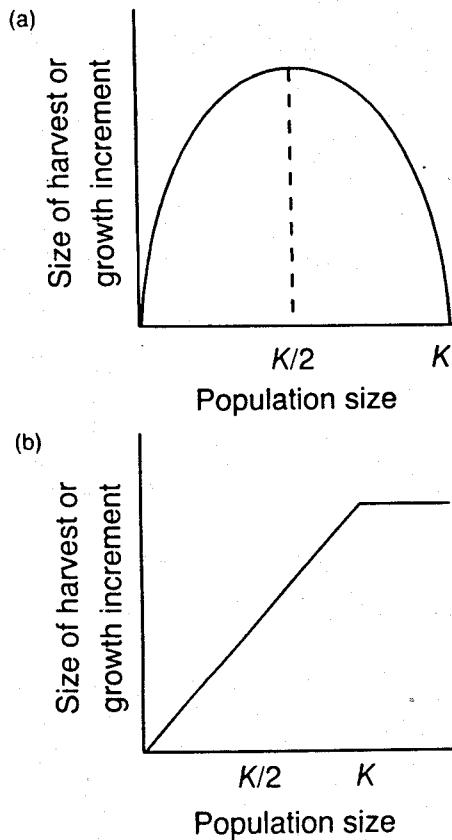


Fig. 7.2. (a) The traditional sustained yield model of harvest as a function of population size. The maximum sustained yield occurs at approximately $K/2$ when population growth is logistic. (b) A hypothetical sustained yield model for harvesting parrot nestlings. Harvest size = annual growth increment as a function of population size. The maximum sustained yield occurs near K . Adapted from Beissinger & Bucher 1992b.

(Beissinger & Bucher 1992b). Manipulating the degree of hatching asynchrony can increase fledging success in some cases, but an understanding of the functional basis of this behavior is required.

Hatching asynchrony

Many birds delay the initiation of incubation until the last egg in a clutch has been laid, causing all eggs to develop and hatch synchronously. If

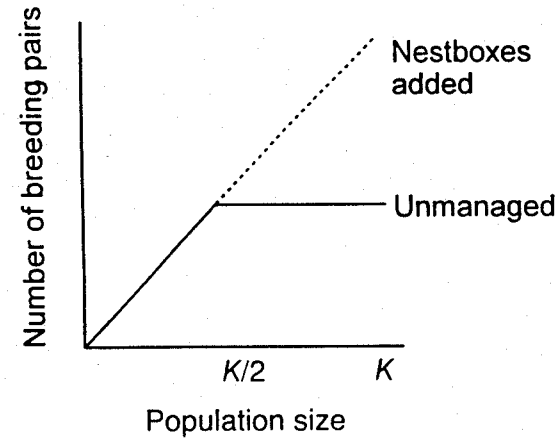


Fig. 7.3. Effect of adding nest sites on the number of breeding pairs when nest sites are limiting, based on the Conservative Harvest Model. Adapted from Beissinger & Bucher (1992b).

parents initiate incubation before the last egg is laid, the result is a staggered hatching of offspring. Asynchronous hatching produces chicks of different sizes in a nest, and frequently results in the mortality of the smallest nestlings (Lack 1947; Stokland & Amundsen 1988; Beissinger & Waltman 1991). Beissinger & Bucher (1992a,b) suggested that because these late-hatched chicks have low probabilities of survival, they may be harvested without adversely affecting the population.

Hatching asynchrony may be applied to sustainable use in other ways as well. The early onset of incubation and resulting asynchronous hatching may serve a number of different functions that reflect different constraints on reproductive success (Stoleson & Beissinger 1995). By identifying the function(s) of hatching asynchrony in a particular species through experimental studies, these constraints on reproduction can be identified. Management actions can then be formulated that address or correct for those particular constraints. Thus, by understanding the function of early incubation behavior, the behavioral ecologist can identify ways to effectively increase productivity in a population.

At least 17 hypotheses have been proposed to explain hatching asynchrony in birds (reviewed in Stoleson & Beissinger 1995). Four categories of hypotheses can be described based on the nature of the selective forces or constraints influencing the decision of when to incubate, and the period(s) in the nesting cycle when those forces or

Table 7.1 Hypotheses for the evolution of hatching asynchrony

Evolutionary significance of asynchrony	Constraint or selective force	Critical period in the nesting cycles	Hypothesis
Non-adaptive	Physiological	Laying	Hormone
		Laying	Energy constraints
Adaptive	Environment	Laying	Egg viability
		Laying	Egg protection
		Laying	Limited breeding opportunities
	Behavior	Laying	Brood parasitism
	Parental efficiency	Nestling	Peak load reduction
		Nestling	Dietary diversity
		Nestling	Larder
	Behavior	Nestling	Sibling rivalry reduction
		Nestling	Sex ratio manipulation
	Environmental Variation	Nestling	Brood reduction
		Nestling	Hurry-up
		Nestling	Insurance
	Behavior	Laying/brooding	Sexual conflict
	Predation	Laying/fledgling	Nest failure
		Laying/brooding	Adult predation

For each hypothesis, the adaptive significance of asynchrony, the nature of the selective force, and the critical period in the nesting cycle are indicated. Adopted from Stoleson & Beissinger (1995).

constraints are relevant (Table 7.1). Two hypotheses suggest there is no adaptive function to either early incubation or the resulting hatching asynchrony; rather, parents are physiologically constrained energetically or hormonally to initiate incubation before the last egg is laid. Four hypotheses posit an adaptive function to the early onset of incubation. The resulting hatching asynchrony is considered incidental, and any offspring mortality resulting from asynchrony would be maladaptive. Early incubation may function to protect eggs or nest sites from unfavorable ambient temperatures, predators, conspecifics, or brood parasites. Eight hypotheses are premised on the idea that asynchronous hatching and the resulting developmental asymmetries among nestlings have an adaptive function. Asynchronous hatching may increase parental efficiency in feeding, or enable parents to deal with stochasticity of food resources or hatching success. Finally, three hypotheses suggest that the timing of the incubation and fledging periods are a response to differential predation through the nesting cycle, or are part of a strategy to

increase male investment by lengthening the time females are on the nest.

Differentiating between these groups of hypotheses to determine the function of hatching asynchrony in any given taxon requires answering several questions. Does early incubation serve to protect the eggs, create an asynchronous hatching pattern, or something else? Does the mortality of small offspring have a function, as with the Brood Reduction Hypothesis, or is it merely incidental? Identifying the function of early incubation and resultant hatching asynchrony can help to identify limits to reproduction. In turn, these limits can indicate potential management actions for increasing productivity, and designing a valid, sustainable harvest program. For example, by experimentally identifying asynchrony as an adaptation to adjust brood size to unpredictable food resources (e.g., Wiebe & Bortolotti 1994), a behaviorist would know that providing supplemental food would be an effective strategy to increase productivity. In this case, it is unlikely that manipulating the degree of asynchrony would have a beneficial effect. This process is better explained through the use of several examples.

Applying hypotheses for hatching asynchrony to sustainable use of parrots

Macaws and the insurance function of asynchrony

Macaws (e.g., *Anodorhynchus* spp., *Ara* spp., *Cyanopsitta* sp.) are among the largest parrots and the most prized in the pet trade. Most species are considered endangered, and some are on the verge of extinction, primarily because of persecution for the exotic bird trade (Yamashita 1987; Collar & Juniper 1992; Munn 1992). Macaws share a number of reproductive traits. They generally lay clutches of 2 to 3 eggs. The smallest chick in a brood rarely survives, even when there is a surplus of food. However, the smallest chick survives if older sibs do not hatch or die very young (Lanning 1991; Munn 1992). Thus, asynchrony in macaws appears to pertain, at least partially, to an insurance function of the smallest chicks.

Understanding the insurance function of asynchrony in macaws has several uses. Because parents rarely raise smallest young, strategies that attempt to reduce offspring mortality may be ineffectual and are unlikely to increase productivity. From a conservation perspective, when the older chicks survive these surplus young can be harvested directly with little or no impact on the population. They represent potential productivity that would otherwise be lost.

Charles Munn and his associates in Manú, Perú, have experimentally harvested the last-hatched young in several macaw species. Chicks were removed from nests at a young age and then hand-raised. They were kept in the area as tourist attractions, however, and never marketed as an economic resource (Munn *et al.* 1991; Munn 1992).

The idea of harvesting small young with low reproductive value has been applied to other species as well. Gyrfalcons (*Falco rusticolus*) are highly coveted by falconers, and like the large macaws, command high prices in the international bird market. Similarly, chicks hatch asynchronously, and the smallest chick functions as insurance (Clum & Cade 1994). The Canadian government has experimented with programs that permitted the harvest of smallest chicks from selected nest sites (Mossop & Hayes 1982). These programs proved biologically and economically feasible, but have been discontinued due to political problems (Clum & Cade 1994). A similar experimental harvest of Prairie falcon (*F. mexicanus*) nestlings resulted in little effect on population parameters or size and appeared to be sustainable over a seven year period (Conway *et al.* 1995).

Parrotlets and the maintenance of egg viability

We have researched the breeding biology and demography of the Green-rumped parrotlet in the llanos of Venezuela. This species is among the smallest of the New World parrots, and one of the few species that may be increasing in number (Forshaw 1989). This species is also unusual because females typically lay large clutches (average = 7, range = 4 to 10 eggs) that hatch completely asynchronously. A clutch of eight eggs may take up to 14 days to hatch (Beissinger & Waltman 1991). Partial brood loss is frequent in larger broods, and the smallest one or two chicks frequently die.

We have tested experimentally a number of hypotheses to determine the function or functions of early incubation that produces extreme hatching asynchrony in this species. We used synchronization experiments (Forbes 1994) to test hypotheses based on the premise that an asynchronous hatching pattern confers some tangible benefit to parents. To summarize the results, we found that broods manipulated to hatch relatively synchronously enjoyed greater reproductive success than natural asynchronous broods, as measured by number and survivorship of offspring (Fig. 7.4). In addition, parents at synchronized broods incurred no detectable costs in terms of effort, survivorship, or impact on future reproduction (Stoleson and Beissinger, in review). Thus, asynchronous hatching in this species appears to serve no obvious adaptive function for

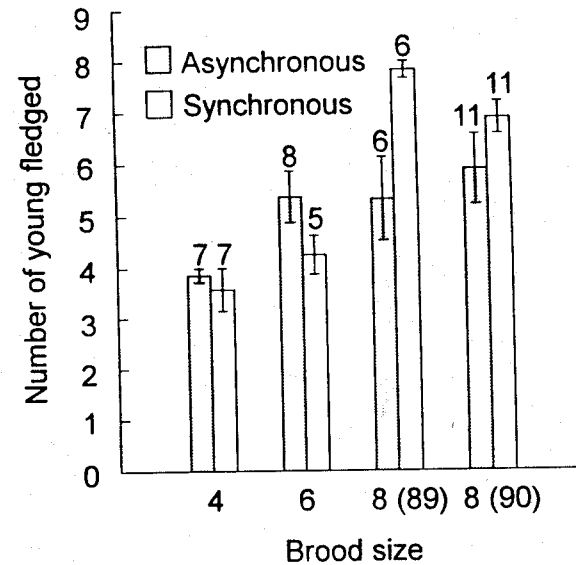


Fig. 7.4. Probability of fledging for Green-rumped parrotlet nestlings from experimental synchronous and asynchronous broods as a function of brood size. Bars indicate one standard error around the mean, and sample sizes appear above each bar. Values exclude depredated nests. Brood size ($F=19.5$, $P<0.001$) and the interaction of brood size and asynchrony ($F=8.1$, $P=0.001$) affected the number of young fledged (two-way ANOVA). Large synchronous broods produced more young than asynchronous broods in 1989 ($t=4.3$, $P=0.003$) and marginally so in 1990 ($t=1.5$, $P=0.15$).

the survival of chicks, and offspring mortality appears to be maladaptive. For parrotlets, therefore, any management techniques that address the problem of offspring mortality associated with asynchronous hatching may increase reproductive productivity. Our experiments specifically demonstrated that reproductive success can be increased by manipulating eggs or young to create broods with reduced degrees of asynchrony (Fig. 7.4).

When we found no evidence to support an adaptive function to asynchronous hatching patterns in the parrotlet, we began testing whether the early onset of incubation confers benefits to parents by ensuring the survival of early embryos. One hypothesis suggests that early incubation functions to maintain the viability of first-laid eggs (the Egg Viability Hypothesis; Arnold *et al.* 1987; Veiga 1992). Embryos begin to develop when eggs are heated above physiological zero (the temperature below which no embryological development occurs, approx-

imately 26–28°C: Drent 1973; Webb 1987). As embryos develop, they become sensitive to changes in temperatures. Prolonged or repeated exposure to temperatures above physiological zero yet below normal incubation levels (34 to 38°C) results in abnormal development or death (Wilson 1991; Deeming & Ferguson 1992). In areas where ambient temperatures regularly exceed physiological zero, embryos may begin to develop in the absence of incubation. Thus, parents may be obliged to begin continuous incubation to maintain the hatchability of first laid eggs.

We tested this hypothesis by removing freshly laid eggs from nest boxes and isolating them in an empty but otherwise identical nest box. After being held for various lengths of time to simulate delays in the onset of incubation, these eggs were placed under incubating females and were incubated to completion. We found that compared with control eggs in recipient nests that were not exposed to ambient temperatures, experimental eggs showed a significant reduction in hatchability with just one day of exposure, and a rapid decline in hatchability with greater exposure times (Fig. 7.5). Thus, there appears to be a physiological basis for the early onset of incubation in the parrotlet.

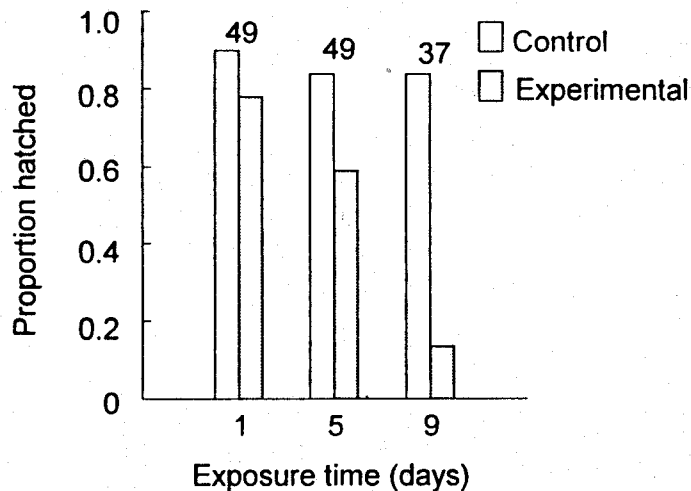


Fig. 7.5. Proportion of experimental parrotlet eggs that hatched in relation to exposure to ambient temperatures prior to incubation for periods of one, five, and nine days, compared with untreated controls. Sample sizes are the number of matched pairs of experimental and control eggs. The probability of hatching did not differ significantly between control and experimental eggs after one day exposure ($\chi^2_1=2.7$, $P=0.10$), but did differ after five days exposure ($\chi^2_1=7.2$, $P=0.007$) and nine days exposure ($\chi^2_1=36.6$, $P<0.001$).

Early incubation to protect limited nest sites

When nest sites are limited in number, parents may be forced to protect the site by initiating incubation early (the Limited Breeding Opportunities Hypothesis; Beissinger & Waltman 1991), particularly in species such as parrots that do not defend general-purpose territories. In our population of parrotlets, behavioral evidence including fights, egg destruction, and infanticide indicate intense competition for nest sites (personal observations). The hypothesis that the early onset of incubation functions to protect eggs from takeover may be tested by placing several parrotlet eggs in empty nest boxes for a period of three days to simulate laying without incubating. Behaviors of individual birds at the site would be observed, and the fate of the eggs followed during the test. Our preliminary results suggest there is strong selective pressure to protect eggs from destruction by conspecifics.

In the parrotlet, the availability of nesting sites appears to be a limiting factor constraining population growth. Although it is difficult to document a change in the number of breeding birds due to the use of nest boxes without carefully structured experiments, evidence suggests the productivity of our study population may have increased considerably since boxes were placed. Parrotlets breed naturally in hollow trees or limbs, termitoriums, or hollowed fence posts (Forshaw 1989; Waltman & Beissinger 1992). At Hato Masaguaral in Venezuela, artificial nest boxes hung on fence posts rapidly became the most used nesting site (Beissinger & Bucher 1992a). The number of nesting attempts in boxes increased from 58 in 40 boxes in 1988 to 181 in 105 boxes in 1994 (Table 7.2). During the same period, no more than 11 nesting attempts per year were recorded in fence posts within the study site. Reproductive success was slightly but not significantly greater (Student's *t*-test, $t = 0.87$, $DF = 15.1$, $P = 0.40$) in successful nest boxes (4.5 ± 1.9 fledglings, $N = 571$ nests) than the successful natural sites (4.1 ± 1.6 fledglings, $N = 15$ nests). Nests in boxes were more likely ($\chi^2 = 9.83$, $DF = 1$, $P < 0.002$) to fledge some young (60%, $N = 971$) than were nests in fenceposts from 1985 to 1994 (34%, $N = 38$). Thus, the addition of nest boxes has increased productivity in parrotlets through an increase in the number of breeders and by increasing reproductive success. Between 1988 and 1994, a total of 2562 parrotlets fledged from nest boxes at this site (Table 7.2). During the same period the number of birds known to have fledged from natural sites was 62, but may have been as high as 95. Increases in productivity through management actions such as these

Table 7.2 Use and success of nest boxes and natural cavities by *Forpus passerinus* in the Llanos of Venezuela 1988–1994

Nest use characteristic	Year						
	1988	1989	1990	1991	1992	1993	1994
No. of nest boxes	40	100	100	100	100	100	105
No. of nesting attempts in boxes	58	119	153	171	173	146	181
No. of successful attempts in boxes	38	56	105	118	108	75	111
No. of young fledged from boxes	156	260	469	483	465	295	507
No. of attempts in natural sites	5	3	3	2	6	6	11
No. of young fledged from natural sites	8	5	5	4	11	10	17

represent potential for harvesting according to the Conservative Harvest Model (Fig. 7.3).

When behavioral studies indicate that nest sites are limiting, the use of nest boxes can allow a greater proportion of birds to breed, and thereby increase productivity (Toland & Elder 1987; Beissinger & Bucher 1992b). Nest boxes have been employed in the management of other parrots (Snyder 1977; Rowley 1990; Munn *et al.* 1991; Mawson & Long 1994), as well as other cavity-nesting species (e.g., Marti *et al.* 1979; Johnson 1987; Caine & Marion 1991; Petty *et al.* 1994).

These examples show that early incubation and asynchrony can have different functions in related species or even in a single species. Simple generalizations across taxa may be inappropriate. Only by experimentally testing appropriate hypotheses can the function(s) of asynchrony in a particular species be determined, and the corresponding constraint on reproduction identified. Once identified, these constraints can be addressed or manipulated to increase productivity and create a harvestable surplus of young. Determining the function of asynchrony in different parrot species is just one area where behavioral studies are needed to guide conservation efforts.

Areas for future research

Parrots are highly social and intelligent animals and display a variety of complex behaviors. Despite increasing interest in wild parrots by both behavioral ecologists and conservation biologists, many aspects of their biology and behavior remain enigmatic. Parrot behavior presents tremendous opportunities for behavioral research that has immediate applicability to conservation.

Aside from our own work, virtually nothing is known of the function or consequences of hatching asynchrony in parrots. A number of species are known to be only partially asynchronous (e.g., Navarro & Bucher 1990; Rowley 1990). Why such variation exists is unclear. In some species, such as the Puerto Rican parrot (Snyder *et al.* 1987), last-hatched nestlings do not suffer reduced survival in spite of pronounced size asymmetries. Further behavioral studies are needed to know if these young somehow differ in quality from older sibs, and how the population might be impacted by their harvest.

Much needs to be learned of mating and reproductive behaviors of parrots. Many of the parrots in the genus *Amazona* will not use nest boxes (Snyder *et al.* 1987). A study of the criteria used in cavity selection in these species is urgently needed and would have immediate application to conservation. The question of why only a fraction of adults in most populations actually breed in any given year also remains unanswered. This issue provides a unique opportunity for research that combines demography, life-history theory, and social behavior. An understanding of this phenomenon might lead to the development of management actions to increase the proportion of breeders, and thus increase the productivity of a population.

The complex social systems and high intelligence of parrots offer particular challenges for conservation. Young birds are slow to learn essential skills such as foraging and predator-avoidance, and appear to require much social contact to successfully acquire these behaviors (e.g., Diamond & Bond 1991; Snyder *et al.* 1994). Although learning and social facilitation in parrots may not be relevant to sustainable use, the success of reintroduction programs may depend on an understanding of these behaviors. For example, recent efforts to reintroduce the Thick-billed parrot (*Rhynchopsitta pachyrhyncha*) in Arizona were hampered by the use of inexperienced birds (Snyder *et al.* 1994).

Some intriguing observations have been published from studies of captive parrots. For example, parent Budgerigars (*Melopsittacus undulatus*) preferentially allocated food to young based on sex or size (Stamps *et al.* 1985, 1987). In several species, pairs were more likely to breed when exposed to certain stimuli, including access to multiple potential nest sites (Shields *et al.* 1989; Millam *et al.* 1995). These results call for behavioral studies of wild birds to verify if these phenomena occur in the wild or are artifacts of captivity.

Conclusion

We brought a theoretically based, multiple hypothesis approach to the question of why parent parrotlets initiate incubation early and consequently hatch their eggs asynchronously. This approach allowed us to test and discriminate among the bewildering number of factors that potentially constrain productivity in parrots by influencing parental incubation behavior. Our research into the constraints on parrot reproduction offers potential insight and direction for population-level management.

Sustainable harvesting of parrots is feasible because the trade in wild birds confers many species with economic value. Harvesting has been tried or proposed for many commercially valuable taxa, including other birds (Feeke 1991), reptiles (e.g., Thorbjarnarson 1991; Werner 1991), mammals (Robinson & Redford 1991b), and plants (Olmsted & Alvarez-Buylla 1995). The concept of sustainable harvesting is probably not an option for the majority of species without recognized economic value. Behavioral studies dealing with the characteristics affecting productivity, survivorship, and other aspects of population demography and regulation, however, can be crucial to developing successful management and recovery strategies other than for sustainable use. As more species become endangered, the need for the expertise of animal behaviorists will become increasingly urgent.

Once a sustainable harvesting program is established, a variety of social, political, and economic problems can impede its viability (Beissinger & Bucher 1992a). Problems may arise with the smuggling of birds on the black market, laundering of illegal birds through legal programs, over-harvesting (especially of large species with low reproductive rates and high market value), and poaching of nestlings from sustained harvest programs. Some of these potential problems can be ameliorated through the development of a reliable marking system to distinguish legal from illegal birds.

Ultimately, the success of sustainable harvest programs depends upon their ability to compete economically with captive-reared birds and with unsustainably harvested birds. Effective regulation of the wild bird trade in importing countries can help to promote the development of sustainable harvest programs. In 1992, the United States passed the Exotic Wild Bird Conservation Act. This Act prohibits the importation of any species listed in the CITES Appendices I, II, III (including all parrots), except for captive-reared birds and those produced by sustainable ranching programs. Although not perfect, it represents a first attempt in dealing

with the problem of continued exploitation by reducing the demand for wild birds and by providing incentives for captive-breeding and sustainable harvest programs.

Conservation problems cannot be solved by scientific solutions exclusively. Biological research can promote an understanding of the systems and organisms we wish to save, but many conservation problems are ultimately political and social. As Meyer & Helfman (1993: p. 570) stated in a discussion of the relevance of ecology to conservation, 'Ecological research is necessary but not sufficient. A better understanding of global ecology will be to no avail without the political will to implement the changes dictated by that understanding.' Even when relevant, behavioral studies may serve no conservation purpose if they are not actively integrated into the policy-making process.

We began the research described here as a behavioral ecology study of the factors that affect the onset of incubation in a bird with extreme hatching asynchrony, knowing only that parrots were endangered, extensively traded, and poorly known. We had no idea that our work would lead to the first detailed study of the potential for sustainable use of parrots. Only when we observed the incredible response of the parrotlet population to our nest boxes did we fully recognize the importance of our work to conservation. Rather than write up our observations for the scientific community to interpret and use, we invested additional time to obtain extra data of direct relevance to conservation. Instead of limiting our audience to fellow behavioral ecologists, we found a much larger community of conservationists and policy-makers hungry for scientists to help them determine if they could wisely incorporate sustainable use into legislation, and an enthusiastic audience when one of us (SRB) testified before the US Congress. To apply behavioral research to conservation involves trade-offs, but the rewards can be gratifying, significant, and long-lasting.

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Chapter 8

Behavioral variation: A valuable but neglected biodiversity

RICHARD BUCHHOLZ AND JANINE R. CLEMMONS

Science linked to human purpose is a compass: a way to gauge directions when sailing beyond the maps . . . but the prudent voyager uses all the instruments available, profiting from their individual virtues.

Kai N. Lee, Compass and Gyroscope

Variation in animal characteristics is used to classify and monitor biological diversity and to establish conservation priorities. Given the magnitude of the extinction crisis, it is understandable that conservationists and policy-makers have attempted to simplify the task of conservation prioritization by adopting traditional systematic methods and taxonomic classifications for organizing biological diversity into conservation units. Unfortunately, behavioral diversity, which is important for the survival of species and contributes to human welfare, is unlikely to be preserved by current schemes of taxonomic classification alone. In this chapter we explore how behavior can be better incorporated into conservation systematics. It is not our intention to discard the use of systematics in conservation, nor do we belittle the contributions of traditional systematics and systematists, past and present, to the protection of nature (Savage 1995). We too lament the deplorable and dangerous decline of taxonomic expertise in universities and museums (Cotterill 1995; Simpson & Cracraft 1995). Nevertheless, for the future, we support a more critical examination of the sole use of theoretical systematics for prioritizing conservation problems. The failure of biologists to agree on a single definition of biodiversity or to identify a single method for measuring biodiversity is indicative of the need to entertain organismal complexity and conservation problems with approaches of great breadth. Along these lines Felds  (1995) has called for “good interaction – a broad-mindedness – all the way from ‘pure science’ to ‘pure application’.” Reliance on any single definition or measurement will fail to achieve conservation biology’s goals. We must strive to develop and implement a multifaceted conservation strategy that includes the assessment of behavior patterns to identify, evaluate, and protect biodiversity in all of its forms.

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