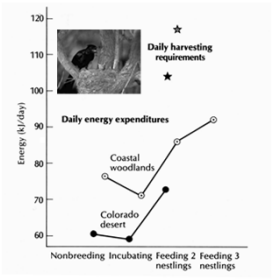
Parental Care, Brood Parasitism, and Cooperative Breeding

Raising a brood is expensive

- Energy expenses can increase by 50% during the breeding season
- Adult Fairy Penguins expend 31% of annual energy during breeding season
- Individual adult birds can feed up to 60% of body mass/day

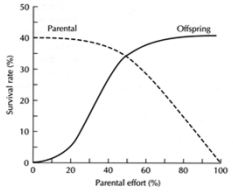


High cost of parenthood favors bi-parental care and monogamy

- Unattended eggs/young are exposed to the weather and predators

Parental behavior reflects competing self interests

- Self interests of males and females, parents and offspring may conflict
- Parental care strategies reflect trade-offs between annual and life time reproductive success



Sinners and Saints?
Brood Parasites and Cooperative Breeders

- Brood parasites and cooperative breeders represent extremes of the parental care spectrum
- They are not cheats or fools, they are individuals subject to natural selection acting in their own self interest

Brood Parasitism

Intraspecific brood parasitism

Within the same species (facultative by definition). Parasitic and non-parasitic individuals are found within the same species. Can occur as a mixed strategy where some individuals parasitize but also rear their own young. Practiced by many waterfowl, ostriches, house sparrows, both yellow and black billed cuckoos, grebes, doves, and gulls among others.

Interspecific brood parasitism

Among different species. Always obligate parasites. Some are quite specialized, e.g. Screaming Cowbird with a single host, others are generalized, e.g. Brown Headed Cowbird has over 200 host species.

Is facultative brood parasitism the first step to obligate brood parasitism?

- Black- and Yellow-billed cuckoos occasionally parasitize one another

Obligate brood parasitism has evolved independently at least 7 times

Anatidae
- Black-headed ducks

Cuculidae
- Old World Cuckoos, 50 spp.
- New World Cuckoos, 11 spp.

Icteridae
- Cowbirds 5 spp.

Indicatoridae
- Honeyguides

Ploceidae
- Indigobirds and Whydas
- Parasitic Weaver

Obligate brood parasites often have very specific hosts

Brood parasite	Primary host(s)
African honeyguides	
Greater Honeyguide	Rollers, starlings, bee-eaters
Lesser Honeyguide	Large barbets, woodpeckers
Scaly-throated Honeyguide	Woodpeckers
Least Honeyguide	Tinkerbirds, small barbets
Cassin's Honeyguide	Rock-sparrows
Wahlberg's Honeyguide	White-eyes, small warblers, flycatchers
Japanese cuckoos	
Common Cuckoo	Great Reed-Warbler, Bull-headed Shrike, Meadow Bunting
Oriental Cuckoo	Eastern Crowned-Warbler
Hodgson's Hawk-Cuckoo	Chats
Little Cuckoo	Wren, Japanese Bush-Warbler

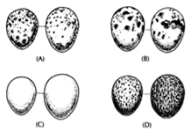
Adaptations of obligate parasites

- Lay more eggs than related non-parasitic species, more energy can be devoted to egg production due to the savings in parental care
- Generalist parasites (cowbirds) lay more eggs (30-40) than specialized parasites (cuckoo and honeyguide lay 15-25)
- Thicker egg shells and larger eggs relative to the host
- Destruction of hosts' eggs and young
  - •Cuckoo adults and chicks remove/eject eggs.
  - •Honeyguide nestlings are born with specialized hooks to kill host's nestlings.
  - •Cowbird and Cuckoo chicks eject host chicks.



Adaptations of obligate parasites

- Mimetic songs, mouth patterns, and egg patterns minimize detection by the host
- Rapid developmental rates (in cuckoos and honeyguides embryo development starts within the females' oviduct) eggs usually require 2 to 4 days less incubation time than hosts
- Genetic information determines song in cuckoos and cowbirds so chicks don't imprint on host species
- Exception is Indigobirds that imprint on their host's song, ensures male and female parasites come from same host (host partitioning)



Effects of parasitism on hosts

- Hosts of specialized parasites (Cuckoos and Honeyguides) normally fledge no young of their own. In contrast, hosts of Indigobirds suffer only slightly from parasitism (mixed broods), while cowbird hosts vary considerably in the costs of parasitism
- Smaller hosts (Indigo Bunting) and those with long incubation periods usually suffer more from parasitism
- Parasitism is less severe at the population level that at local or individual levels.
- Traditional models for parasite-host interactions apply. These models predicts that parasitism will eventually stabilize at a low levels (dynamic equilibrium)
- Alternatively "evolutionary arms race" cycles, were the parasite gets more virulent and the host more defensive, may also evolve

Host defenses

- The severe costs of parasitism select for host defenses
  - Direct
    - Rejection or puncture of parasite eggs, e.g. American Robins
    - Ejection of nestlings (many species)
    - Yellow Warblers bury cowbird eggs (success higher than deserted or accepted nests)
  - Indirect
    - Aggressive defense of nest and mobbing of parasites (solitary and colonial species)

TABLE 19–2
Nesting success of parasitized Yellow Warblers

Nest status	Number of nests	Nest success[a]
Parasitized		
Buried	13	0.78
Deserted	10	0.00
Accepted	12	0.53
Not parasitized	64	0.80

a. Average number of fledged young per egg laid, including buried eggs.
After Clark and Robertson 1981.

Cowbirds invade

Brown-headed 1700

Shiny 1890

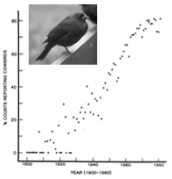
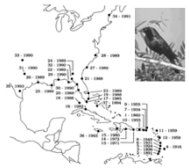


TABLE 5. Frequencies of nest parasitism of forest birds which build open cup nests and accept cowbird eggs for all three woodlots combined. Data include nests that were not monitored for predation (Table 3)

Species	Nests[a]	Percentage parasitized	Average number of host eggs/ nest (n)[b]	Average number of cowbird eggs/nest (n)[c]	Average number of cowbird eggs/parasitized nests (n)
Eastern Wood-Pewee	3	67	2.0 (1)	2.0 (1)	2.0 (1)
Acadian Flycatcher	2	50	2.0	1.0	1.0 (1)
Wood Thrush	19	100	1.2 (15)	4.6 (15)	4.6 (15)
Kentucky Warbler	6	33	3.5 (4)	0.5 (4)	1.5 (1)
Ovenbird	5	40	3.6 (5)	1.0 (5)	2.5 (2)
Louisiana Waterthrush	0	50	–	–	–
Northern Cardinal	20	55	3.4 (16)	1.2 (16)	1.7 (11)
Rose-breasted Grosbeak	1	0	3.5 (2)	0.0 (2)	–
Rufous-sided Towhee	2	50	3.0 (1)	1.5 (2)	3.0 (1)
Scarlet Tanager	4	75	3.0 (3)	3.5 (3)	5.0 (1)
Summer Tanager	6	100	1.3 (4)	3.5 (4)	5.5 (4)
Total	75	67.1			3.5 (50)

a. Total number of nests found.
b. n = number of nests with eggs.
c. n = number of parasitized nests.



Chestnut-headed Oropendolas

- Oropendolas (top) nest in colonies in Central and South America, high mortality of nestlings due to bot fly maggots
- Oropendolas allow parasitism by Giant Cowbirds (bottom) in colonies with high infections of flies because cowbird nestlings pluck fly maggots off of oropendola chicks
- Oropendolas eject cowbird eggs in colonies without flies
- Cowbirds lay non-mimetic eggs (C) in colonies affected by flies, in colonies without flies cowbirds are secretive and produce mimetic eggs (B)
- Oropendolas also nest close to wasps and bees that predate adult flies

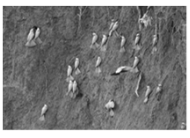
Cooperative breeding

Occurs when individuals other than the parents provide parental care for the young

Helpers usually are young, non-breeding individuals, often previous offspring or relatives

Forms of cooperative breeding

- Breeding pair with various helpers (up to 6): Florida Scrub Jay
- Multiple breeding females in one nest: (Groove-Billed and Smooth Billed Anis)
- Complex societies: White fronted Bee Eaters



Why help?

- Enhance reproductive success
- Enhance production of relatives "kin selection"
- Learn essential skills for parental care
- Reduced predation (more eyes watching)
- Enhances survival of parents
- Ability to re-nest sooner
- Increase potential to find a mate nest site or territory
- Helpers receive help in return - "reciprocal altruism"

Is helping evolutionary nonsense?

Some scientists (including Darwin!) have argued that altruism can't be explained by natural selection.

This is not true when we consider that natural selection will favor any behavior that benefits survival and reproduction.

Ecological constraints drive some species to cooperate until they have a chance to reproduce themselves.

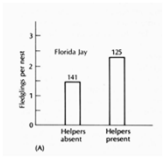
Limiting factors that promote cooperation include; female scarcity, scarce suitable habitat, or scarce and unpredictable food resources.

- Scarce suitable habitat increase the risks of dispersal by young and may trigger cooperative breeding (Red-cockaded Woodpecker)
- Pied Kingfisher in lakes of Kenya breeds cooperatively only on lakes with low prey abundance
- Seychelles Brush-Warbler stopped breeding cooperatively when it was transplanted to a neighboring island with more suitable habitat

Cooperative Breeders

Florida Scrub Jay

- Exists only in "islands" of oak-palmetto scrub in central Florida
- Available habitat is saturated with territories
- Females disperse and wait for opportunities to enter breeding population as helpers, they monitor nearby groups to replace disappearing breeding females
- Males wait to inherit breeding positions in natal territories
- Dominant older sons replace their fathers, stepfathers or brothers



Woolfenden and Fitzpatrick (1984)

Red-cockaded woodpecker

- Depend on cavities dug in old longleaf pines
- Flowing sap protects from predators
- Cavities take a long time to excavate and are a limiting factor for populations

Note: in both species Females disperse, Males inherit.

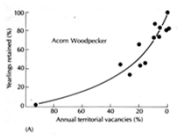
Cooperative breeding often reflects limited resources

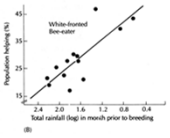
Acorn Woodpeckers

- Depend on communal granaries
- When territories fill up best option is to be a helper

White Fronted Bee-Eaters

- Breeds in large colonies but functions in small clans of 2 to 7 individuals
- Clans defend a common territory
- Members of each clan breed, feed, and roost as a cooperative group
- Individuals appear to remember past associations
- Individuals leave groups to join new ones, but can go back to the old clans years later
- Helping is a function of habitat quality





Demography and Populations

- Demography is the study of fecundity and survival
- Four critical variables
  - Age of first breeding
  - Number of young fledged each year
  - Juvenile survival
  - Adult survival