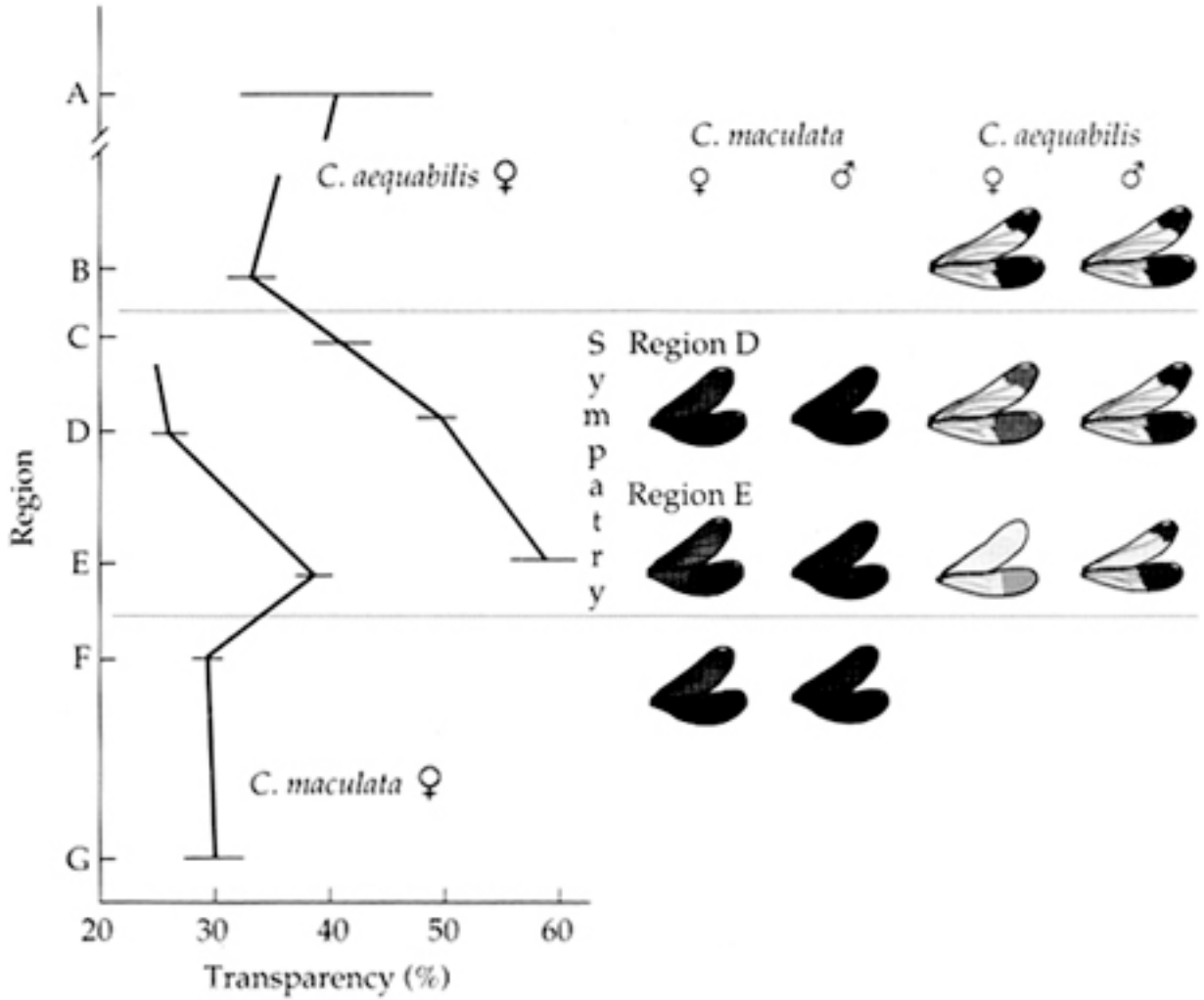
Mating Games and Signalling

- Reading: pp 571-592, ch 23
- Signal design for mate attraction and courtship
- Searching vs signaling for mates
- Courtship control and persistence
- Mechanisms of mate choice

Mate attraction signal rules

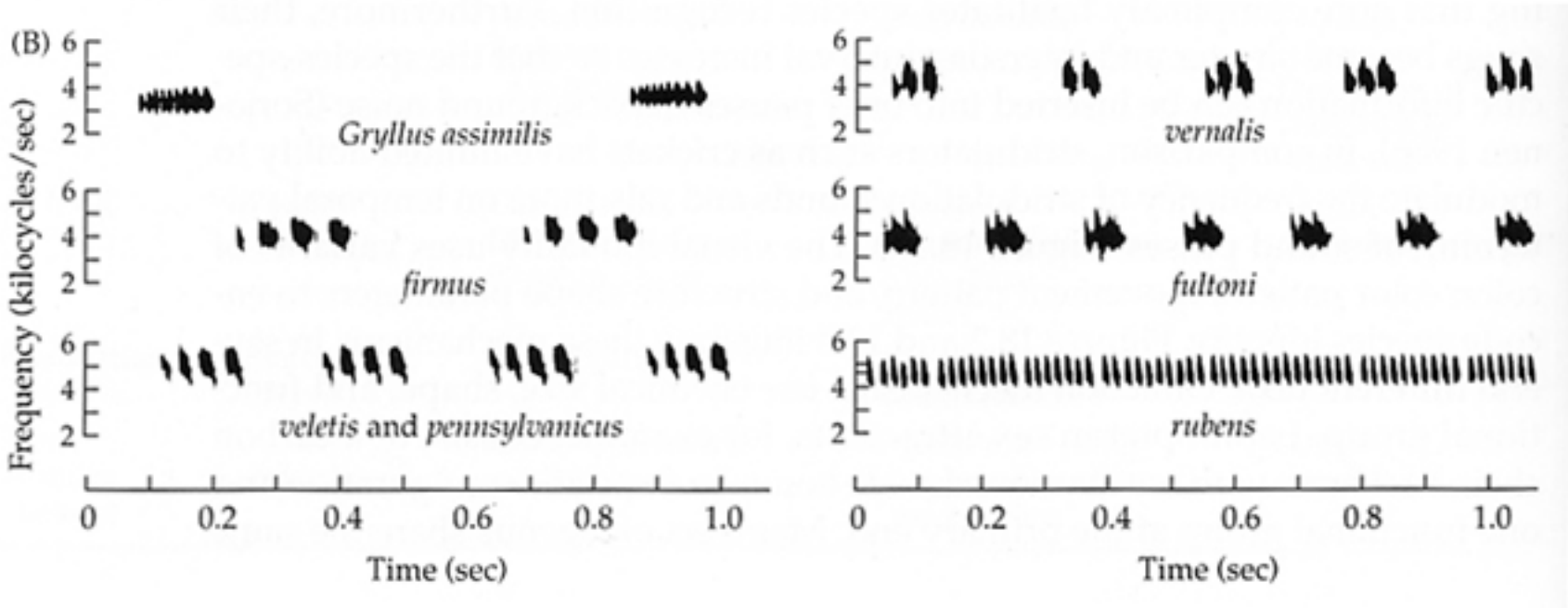
- Signals designed to attract potential mates from a distance
  - large signal range
  - high locatability
  - high duty cycle
  - species specific
  - stereotyped (low modulation level)
  - arbitrary form-content linkage

Character displacement in damselflies



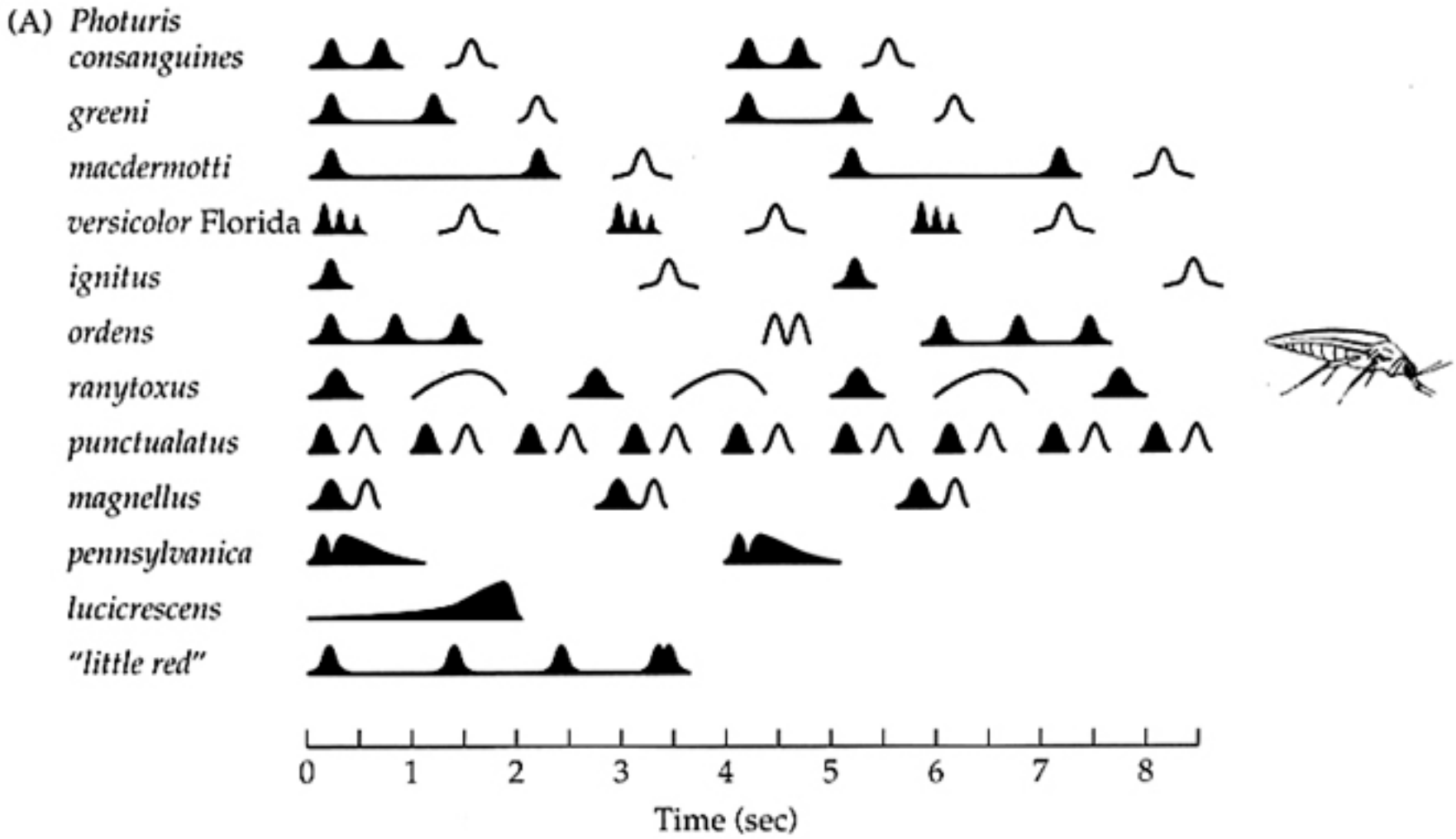
Expect species specificity of mate attraction signal when females emit the signal since they have more to lose from a hybrid mating

Species differences in cricket calls

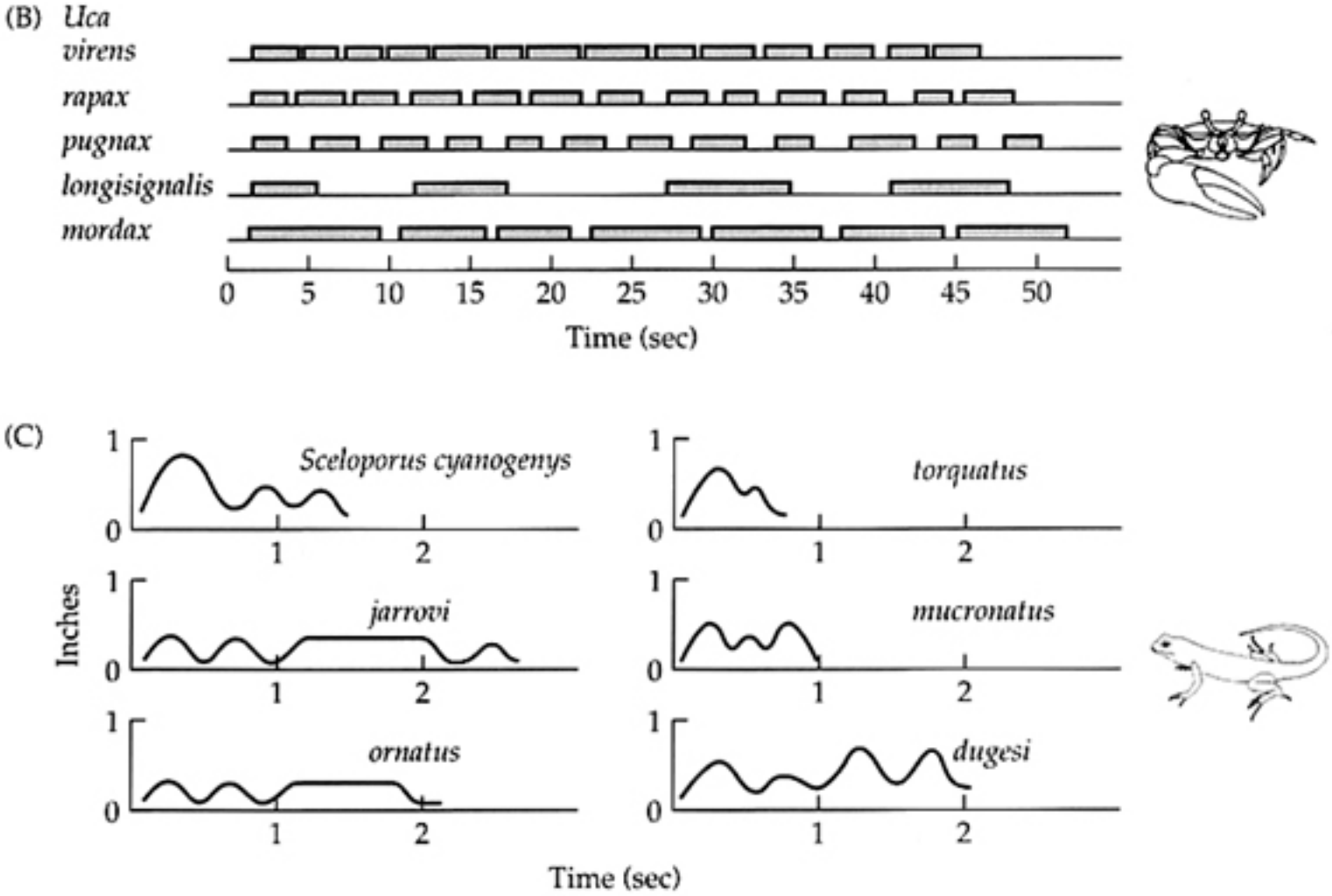


Species differences are encoded in temporal patterns

Species differences in firefly flashing signals



Species differences in fiddler crab and fence lizard displays



Martins, E.P., Labra, A., Halloy, M. & Thompson J.T. (2004) Large-scale patterns of signal evolution: an interspecific study of *Liolaemus* lizard headbob displays. *Animal Behaviour 68:453-463*

Species differences in facial patterns

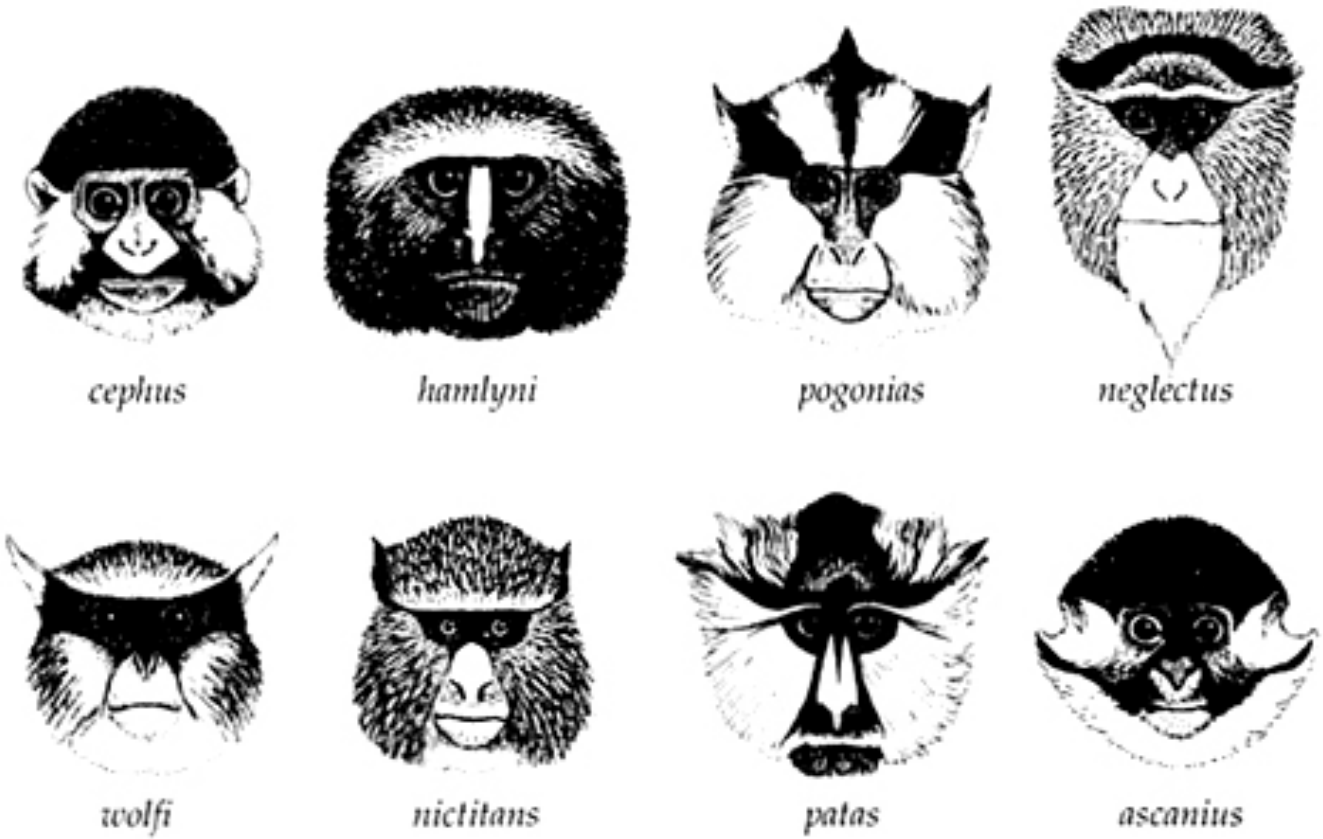
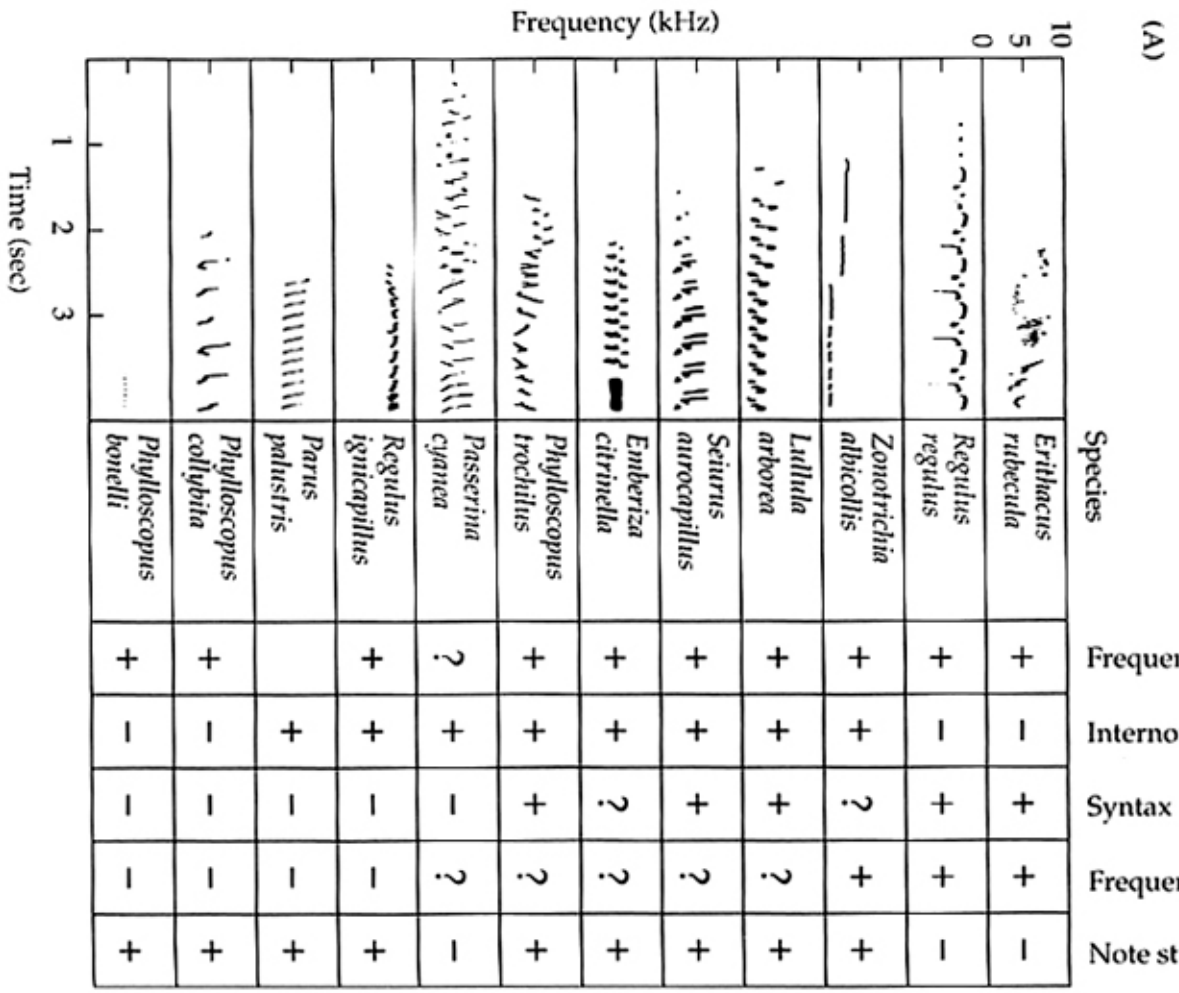


Figure 18.3 Facial color patterns in African guenons. African guenons in the genus *Cercopithecus* often live in mixed species troops and use conspicuous, colorful skin spots and hair tufts as the primary species recognition mechanism. The colors used include white, black, brown, yellow, blue, and red. (After Kingdon 1988.)

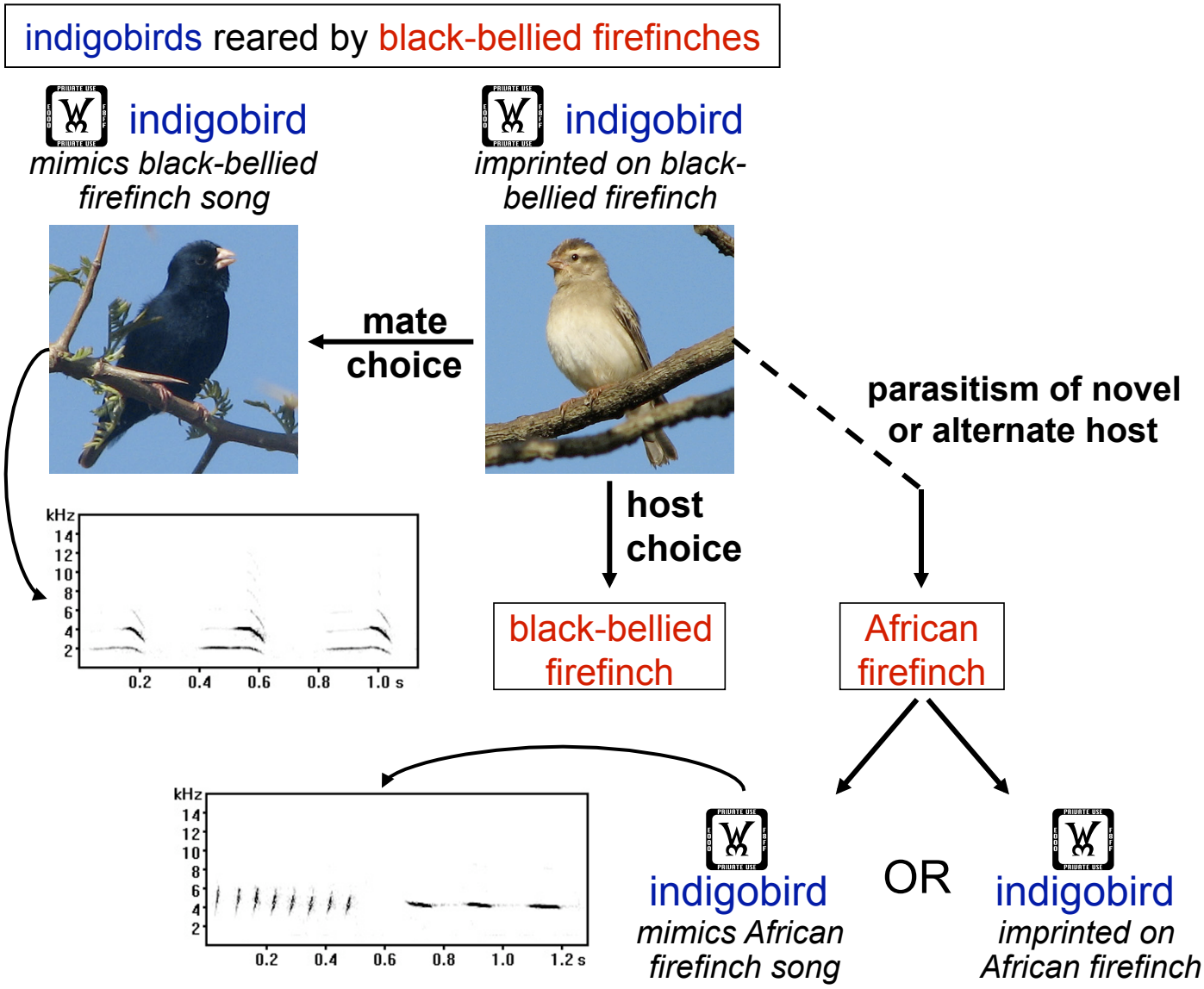
Species differences in bird song



Species	Frequency range	Internote interval	Syntax	Frequency changes	Note structure
Erithacus rubecula	+	I	+	+	I
Regulus regulus	+	I	+	+	I
Zonotrichia albicollis	+	+	?	+	+
Lullula arborea	+	+	+	?	+
Seiurus aurocapillus	+	+	+	?	+
Emberiza citrinella	+	+	?	?	+
Phylloscopus trochilus	+	+	+	?	+
Passerina cyanea	?	+	I	?	I
Regulus ignicapillus	+	+	I	I	+
Parus palustris		+	I	I	+
Phylloscopus collybita	+	I	I	I	+
Phylloscopus bonelli	+	I	I	I	+

Species differences are encoded in frequency range, INI, note structure

Sexual imprinting and sympatric speciation



SORENSON, M. D., SEFC, K. M. & PAYNE, R. B. (2003) Speciation by host switch in brood parasitic indigobirds. *Nature*, 424**,** 928-931.

Convergence in mate attraction signals

- Habitat effects
  - Bird song
    - whistles in forest, trills in open habitats
  - Lizard head bobbing
    - bob shape on ground, interbob interval for arboreal species
- Signaling sex and modality
  - Males tend to use auditory or visual signals
  - Females more likely to use chemical signals

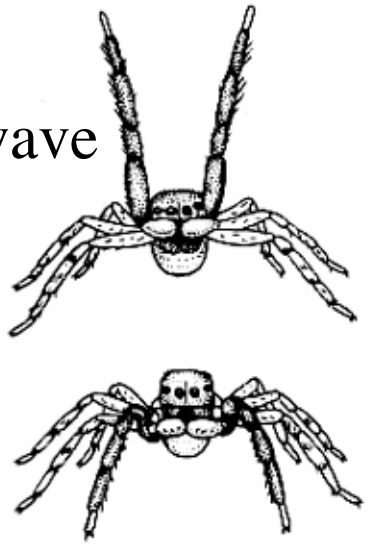
Courtship signal design rules

Table 18.3 Design rules and modality-specific mechanisms for courtship signals

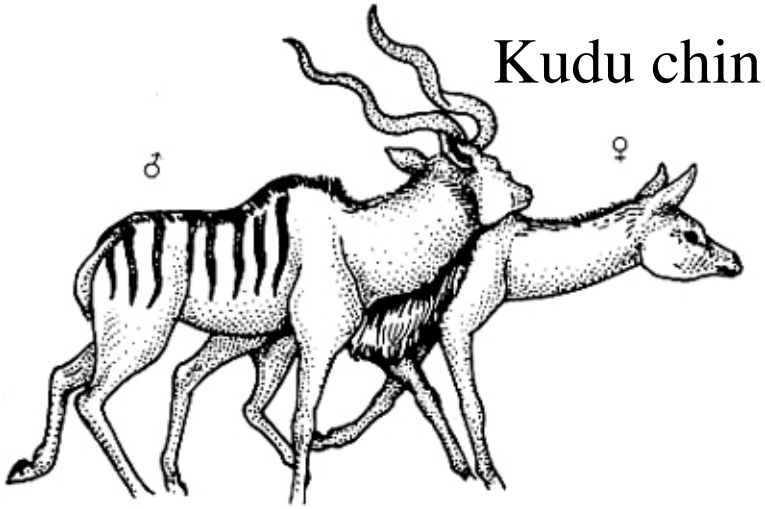
Design feature	Rule	Visual mechanisms	Auditory mechanisms	Olfactory mechanisms	Tactile mechanisms
Range	Short	Low color contrast Subtle movement display	Soft unstructured sounds	Contact chemical Volatile, rapid fadeout chemical	By definition
Locatability	Receiver and Nest site	Directed display Pointing	Beam sound Countercalling	Directed flow Add visual component	Herding
Duty cycle	High for short period	Flashing color High display repetition rate	High repetition rate	Contact chemical	Hold High touch rate
ID level	Species and Sex	Sexual dimorphism	Sex-specific sound pattern	Sex-specific chemicals	Sex specific pattern
Modulation level	Graded	Display rate	Repetition rate	Poor	Vary pressure
Form-content linkage	Linked: Intentions Parent skill Stimulate Calm	 Nesting behavior Courtship feed Submissive	 High frequency Repertoire Soft warble	 Receptivity Hormone manip Tranquilize	 Mount Nuptial gift Lick genitals Stroke

Form-content linkage in courtship

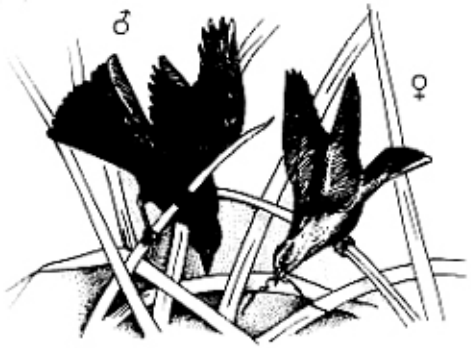
Male leg wave



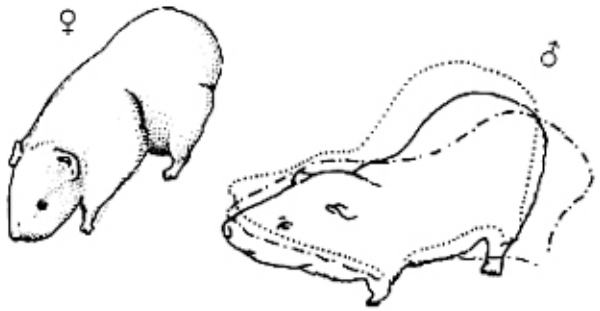
Kudu chin push



Blackbird points to nest

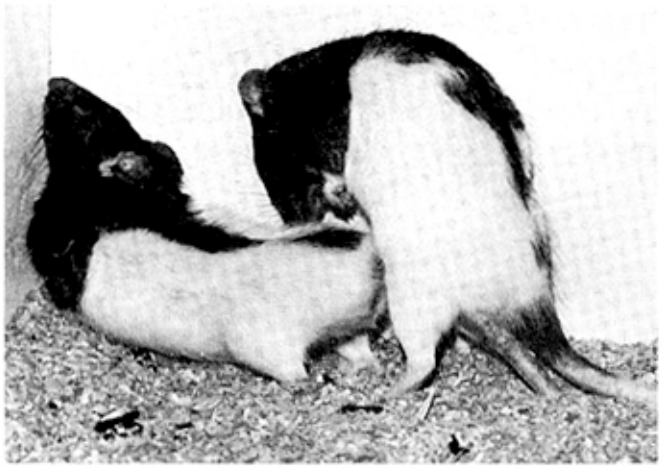


Guinea pig rumba dance



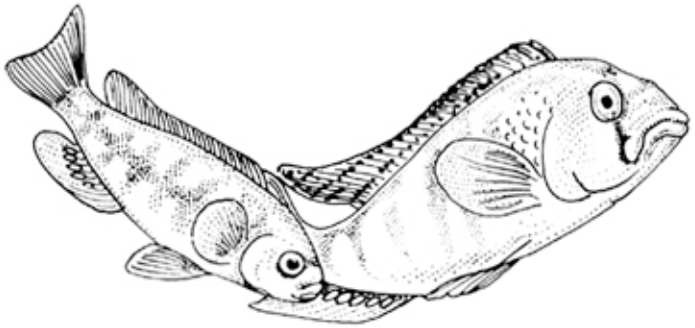
Courtship can facilitate copulation synchronization

(A)

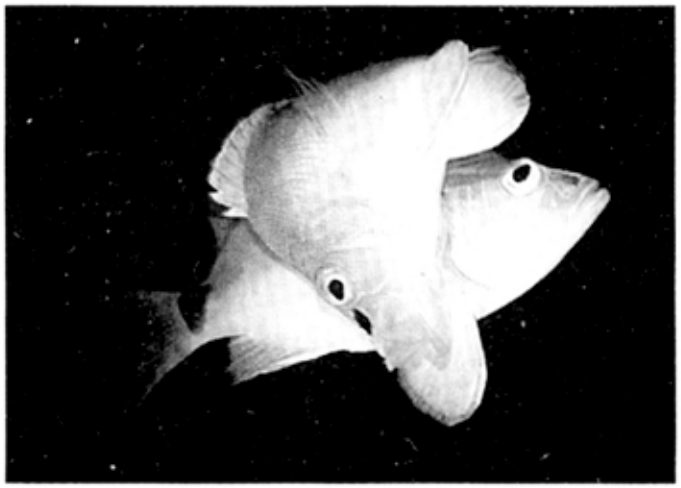


(B)

C)



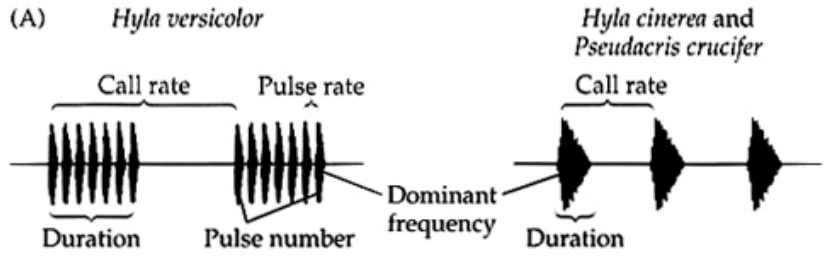
(D)



Static vs dynamic calling displays in tree frogs

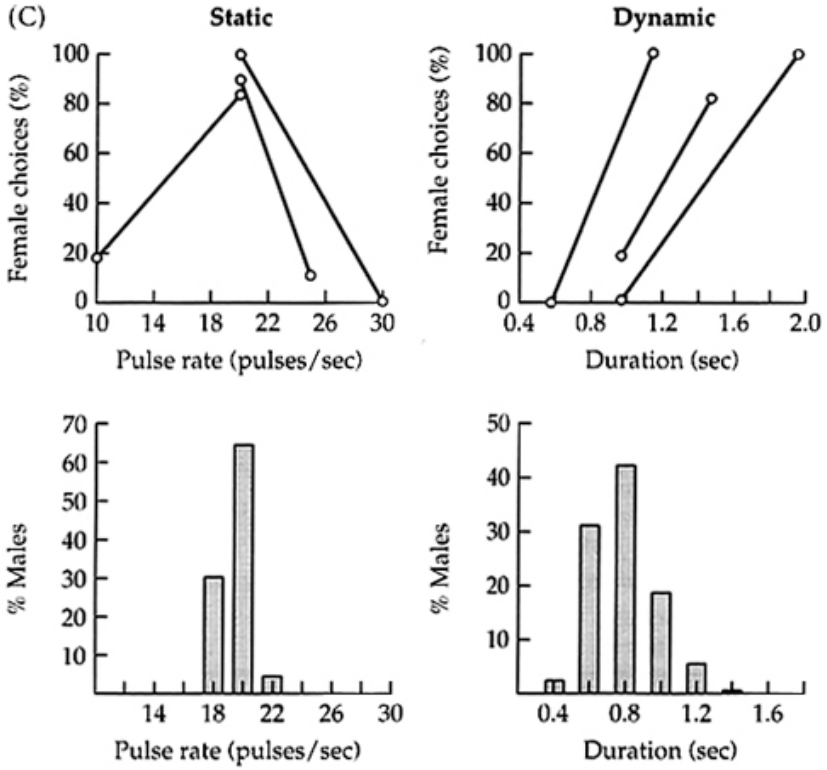
Static components:
Convey information about species differences.
Females prefer mode.

Dynamic components:
Convey information about individual differences.
Females prefer extremes.



(B)

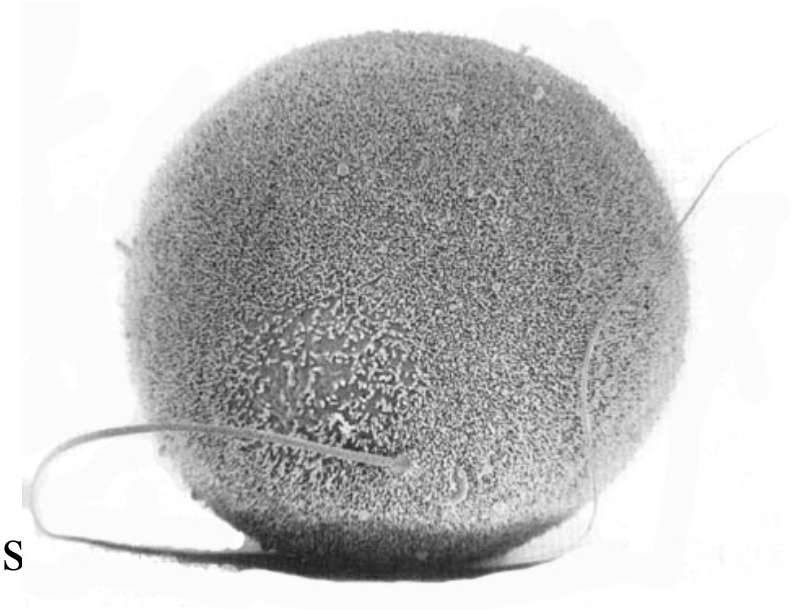
	Dominant frequency	Pulse rate	Call duration	Pulse number	Call rate
H. versicolor	0.8	1.5	16.4	15.0	25.4
H. cinerea	0.5		3.7		12.3
P. crucifer	0.8		4.0		16.0



Sexual selection and signalling

- Mate attraction and courtship signalling is influenced by
  - The operational sex ratio
  - The male mating strategy
  - The relative importance of intrasexual (male-male competition) vs intersexual (female mate choice) selection

Consequences of anisogamy

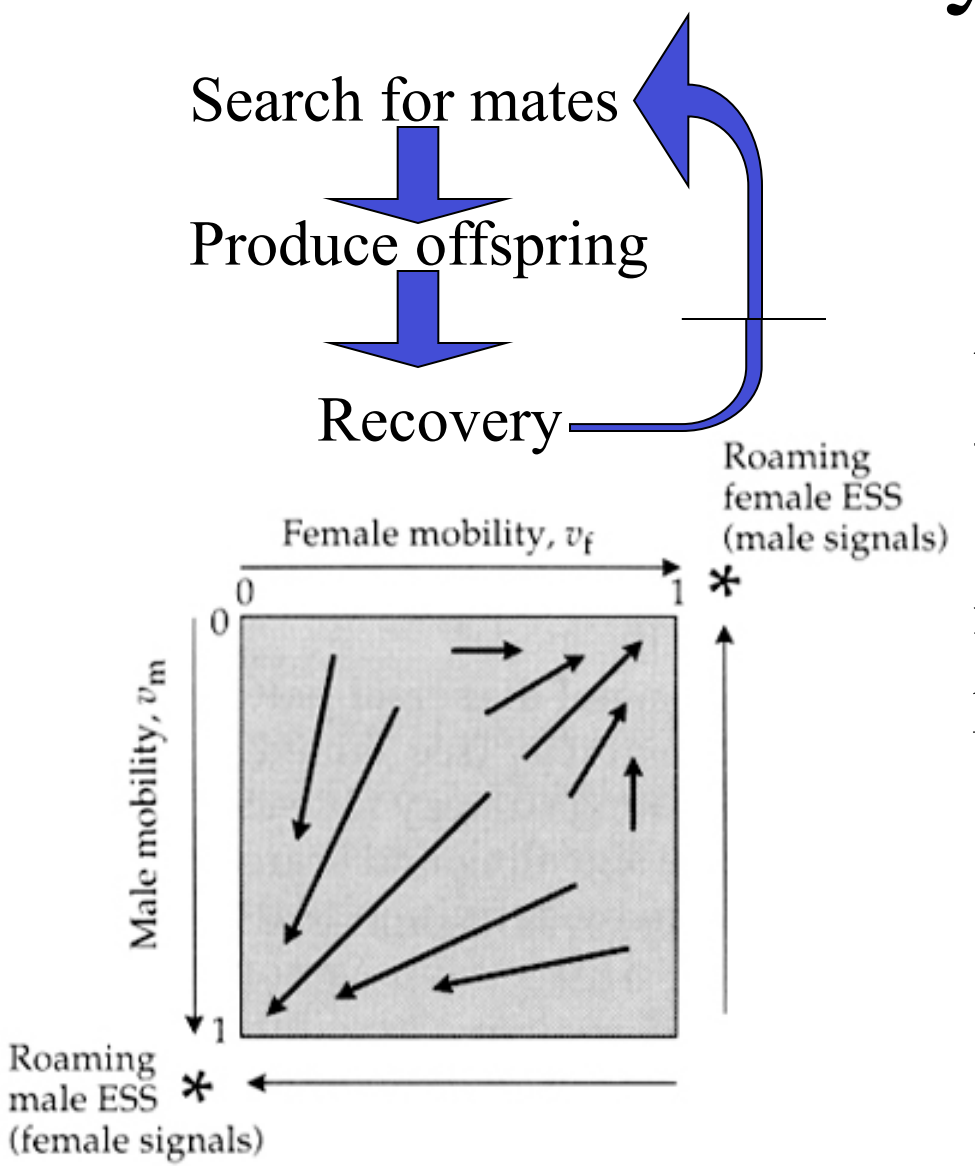


- Females produce few costly, large, immobile, and well-provisioned eggs
- Males produce many small mobile sperm, and can fertilize many females
- Males compete for access to receptive females
- Sedentary males compete by sperm competition (e.g. sea urchin)
- Mobile males can either search for females, defend resources, or wait for females to encounter them (most vertebrates)

Male mating strategies

- If sedentary, compete by sperm competition
  - equip gametes for competition
  - produce many gametes
- If mobile, strategy depends on resource distribution
  - Search for and defend females
    - long-term association(monogamy or permanent harem)
    - dominance hierarchy determines access to females
    - short-term associations during receptive period
    - coercion
  - Defend resources needed by females
    - breeding or feeding sites
  - Advertise to attract females
    - display on leks

Mobility game



- Continuous asymmetric scramble with equal sex ratio
- Operational sex ratio skewed towards sex with shortest gamete + recovery time
- Each sex seeks strategy that minimizes its cycle time given partner behavior
- 2 ESS's: male search and female signal or female search and male signal
- Male searching more common due to female costs

Mate searching patterns

Males tend to search if female location is predictable

Females tend to search when there is resource defense since males are tied to resources

Nonsearching sex emits attraction signals

Exaggerated signals are given by males due to sexual selection

Table 23.2 Patterns of searching sex, long-distance advertising sex, and mating system in a variety of mobile animals

Taxon	Searching sex	Signaling sex and modality	Mating system
Insects			
Crickets, katydids, grasshoppers, cicadas	F	M/Aud	Burrow defense, nuptial gift or self-advertisement
Bark beetle, carrion beetle, boll weevil	F	M/ Olf	Oviposition site defense or self-advertisement
Hawaiian *Drosophila*, fireflies, hill-topping and swarming species, dragonflies	F	M/Vis	Self-advertisement or oviposition site defense
Some bees, other nectivores, parasitoids, dung beetles	F	none	Defense of food sites, males grab females
Most moths	M	F/Olf	Female defense
Many Hymenoptera, Diptera, some butterflies, scarab beetle	M	none	Males wait at female emergence site
Many butterflies, solitary bees	M	F/Vis	Female defense, male patrolling
Fish			
Reptiles and Amphibians			
Urodeles	M	F/Vis	Female defense
Anurans	F	M/Aud	Oviposition site defense or self-advertisement
Lizards	M	F/Vis	Resource defense
Geckos	F	M/Aud	Resource defense
Snakes	M	F/Olf	Female defense
Birds			
Most songbirds, many nonpasserines	F	M/Aud + Vis	Resource defense or self-advertisement
Ducks, geese	M	M/Vis	Female defense
Some corvids, quail	M	F/Aud	Female defense
Mammals			
Most primates	M	F/Olf + Vis	Female defense
Chimpanzee, gorilla	F	M/Aud	Resource defense
Most rodents	M	F/Olf	Female defense
Pika, house mouse, white-lined bat	F	M/Aud + Olf	Resource defense
Horses	M	F/Olf.	Female defense
Most ungulates	F	M/Vis + Olf	Resource defense

Source: Greenwood 1980; Thornhill and Alcock 1983; Macdonald 1984.
Note: Aud = auditory; Olf = olfactory; Vis = visual.

Courtship duration patterns

- Females control courtship in male resource defense and self-advertisement systems
  - courtship prolonged, involves many male displays
  - e.g. most birds, lekking and paternal care species
- Females also control courtship in predatory species
  - Male signals often submissive
  - e.g. spiders, preying mantis, lions
- Males control courtship in female defense systems
  - courtship is often short or absent, or may be aggressive and violent in male dominance systems
  - some insect males mate with females before eclosion
  - some bats mate while females hibernate
  - some sea slugs use “love darts”- hypodermic penises

Mechanisms of mate choice

- Direct benefits (choice influences mate fecundity or survival)
- Indirect benefits (genes passed to offspring)
  - Fisher's process - predicts arbitrary traits
  - Good genes - predicts traits indicate genetic quality
    - Condition dependent indicator traits
    - Revealing indicator traits

Direct benefits of assortative mating in Australian frogs

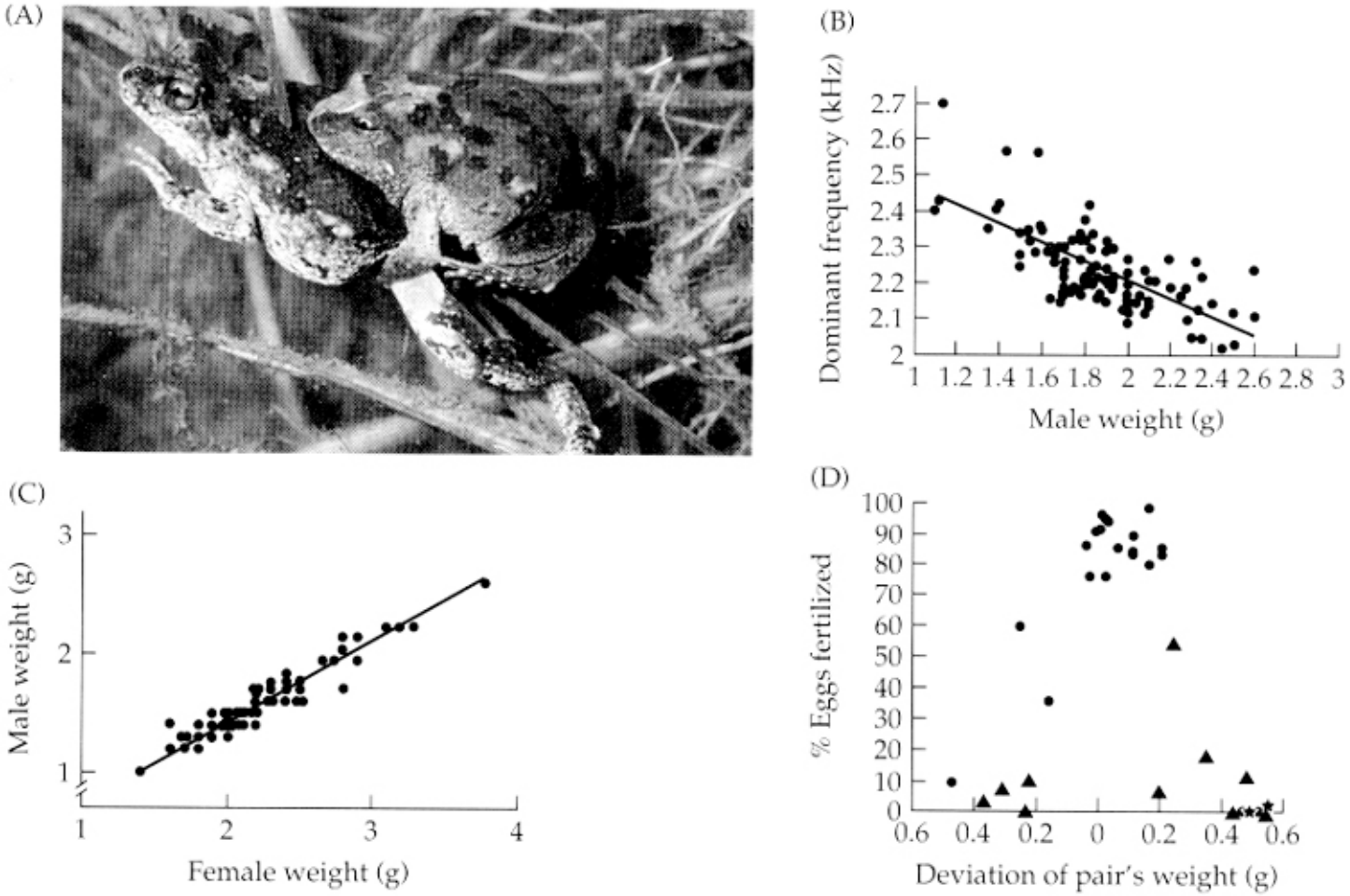


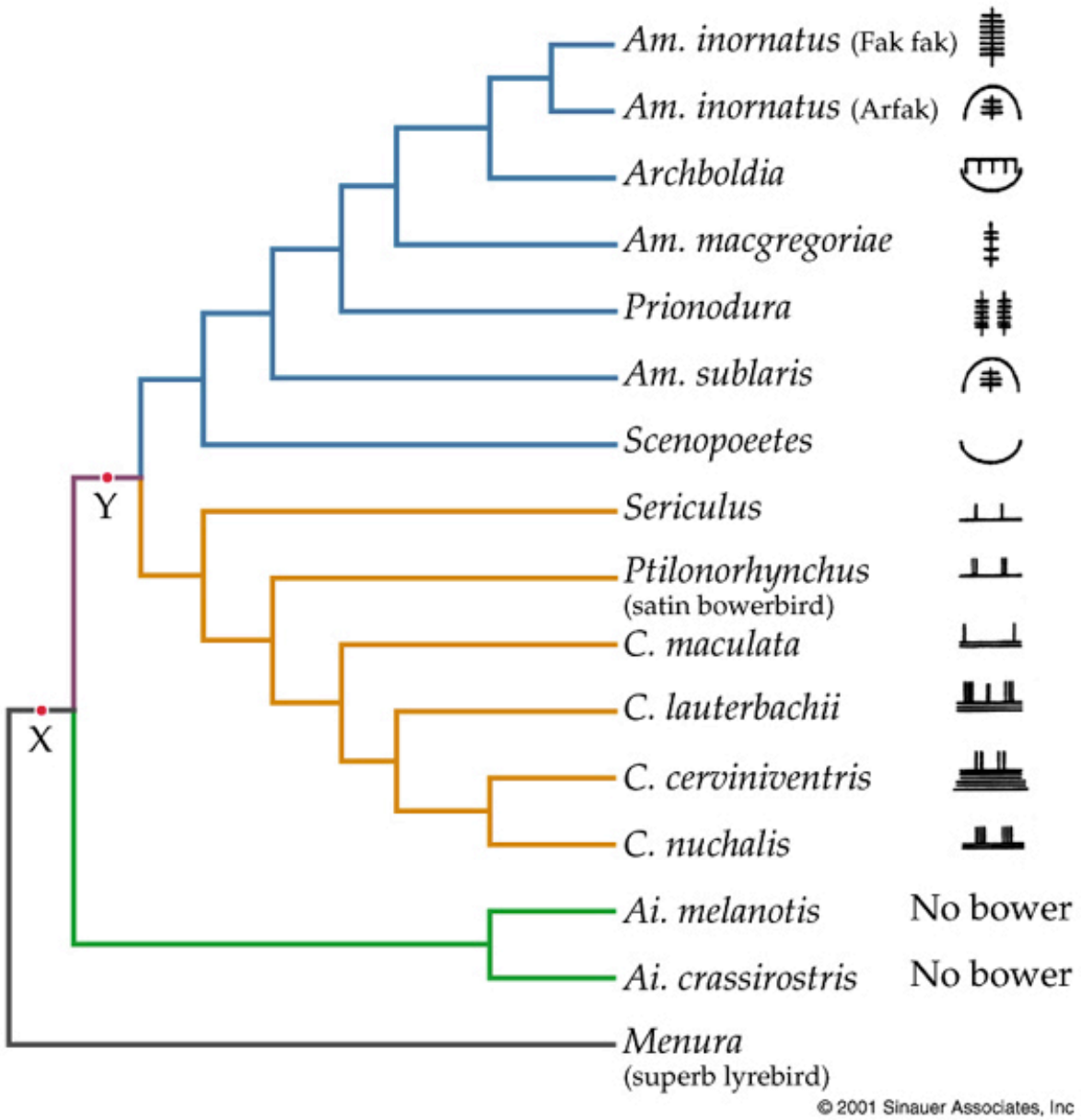
Figure 23.11 Benefits of female preference for call frequency. In the Australian frog *Uperoleria*

Fisher's runaway process

- If
  - a female exhibits preference for a male trait, and
  - there is no cost to females to express this preference
- Then
  - both sons and daughters of this female will carry genes for both the preference and the trait
  - This creates a genetic correlation between preference and trait
- This correlation between preference and trait
  - leads to a "runaway" increase in the male trait until
  - further increase in the male trait is opposed by natural selection
- Predicts extravagant, arbitrary traits

Arbitrary traits in birds-of-paradise?

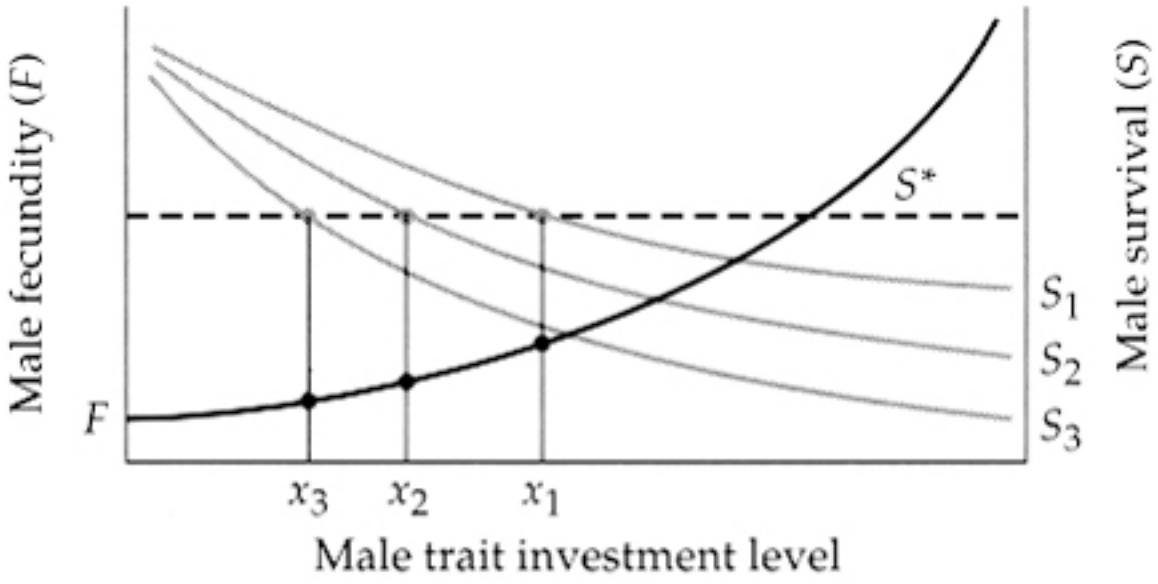
Population variation in bowers



Good genes models for female choice

- Females do not get direct benefits from males
- Females choose males with best overall genetic quality in order to maximize offspring viability
- Predicts mating signals that depend on male condition and thereby indicate male quality
  - Assumes that male quality is heritable

Condition dependent trait

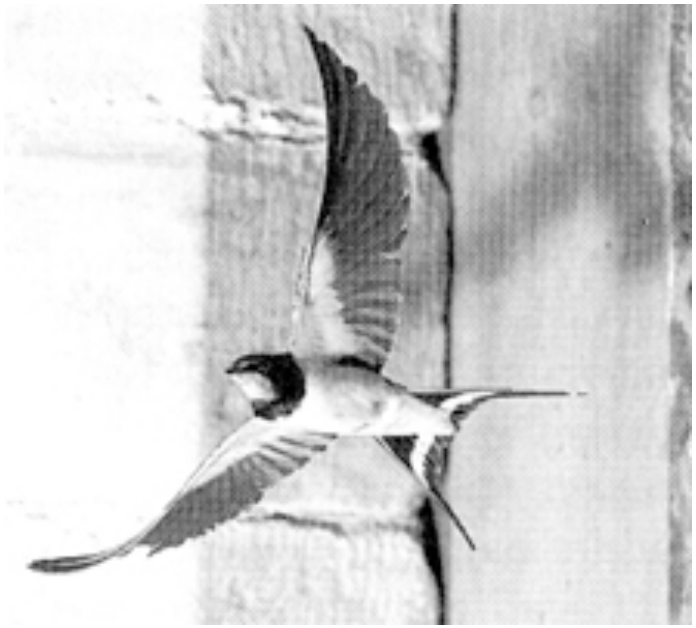


At equilibrium:
$x_1 > x_2 > x_3$
$F_1 > F_2 > F_3$
$S_1 = S_2 = S_3$

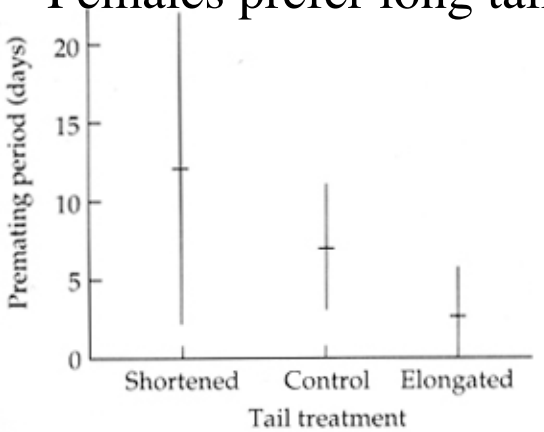
- Fecundity at ESS
- Survival at ESS
- - - ESS

Only males in good condition can make a large investment in a trait which then has less affect on their survival

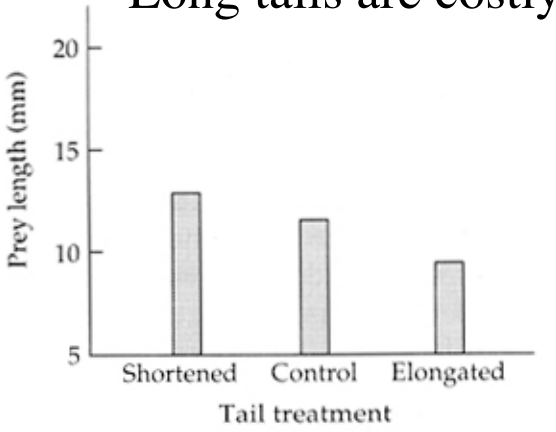
Barn swallow tail length indicates parasite resistance



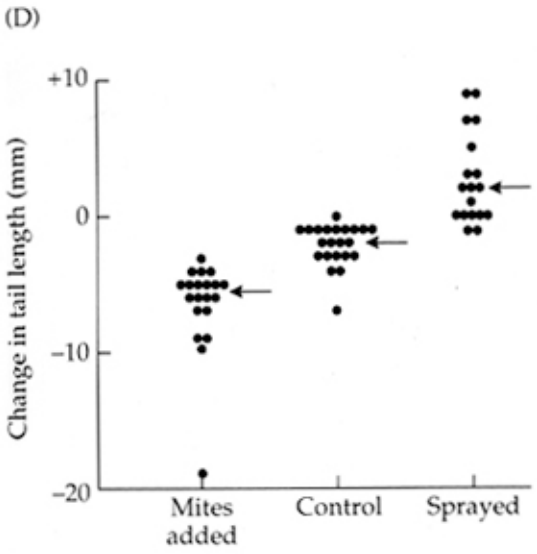
(B) Females prefer long tails



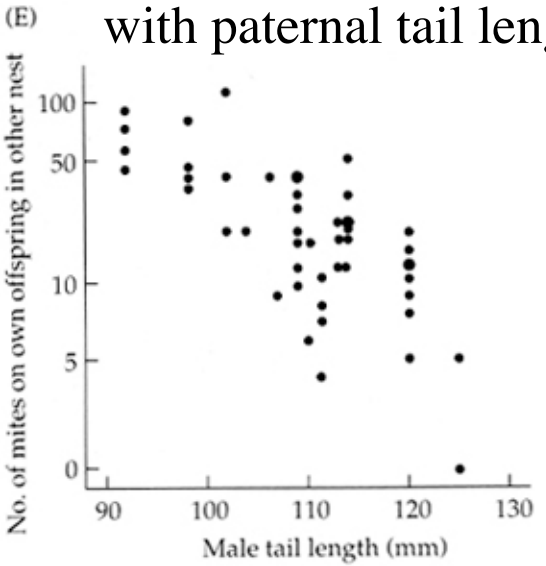
(C) Long tails are costly



Parasites influence tail length



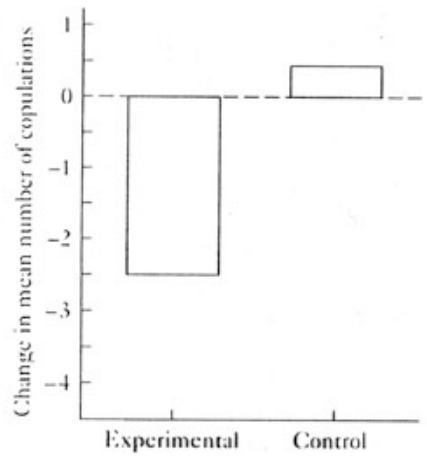
Resistance correlates with paternal tail length

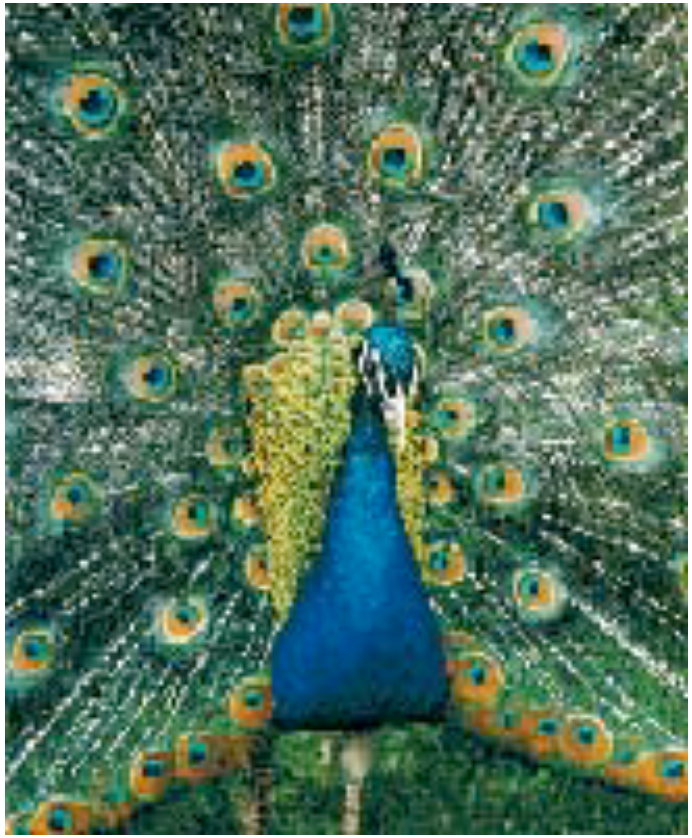


But, males do provide parental care and tails may improve flight

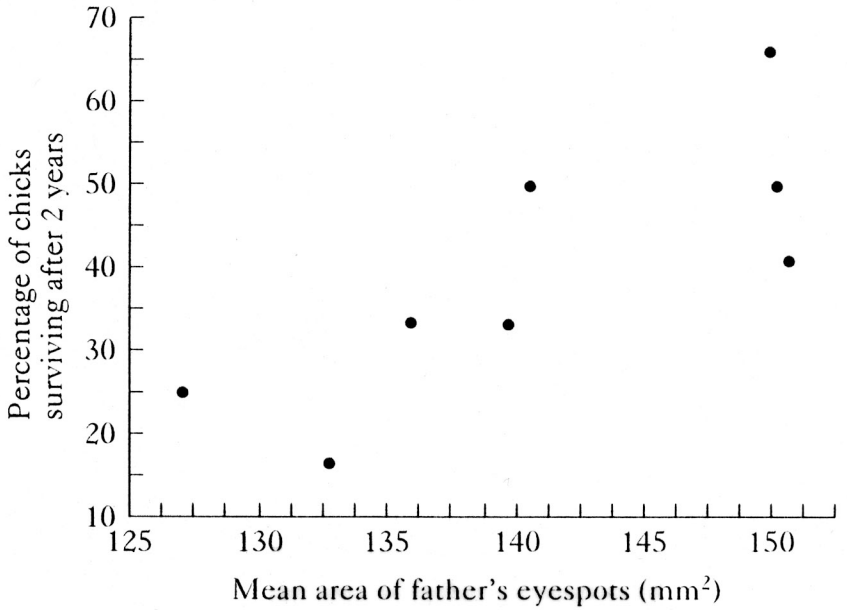
Bro-Jorgensen J, Johnstone RA, Evans MR 2007 Uninformative exaggeration of male sexual ornaments in barn swallows. CURRENT BIOLOGY 17: 850-855

Effect of spot removal on mate success





Do peacock trains indicate male quality?



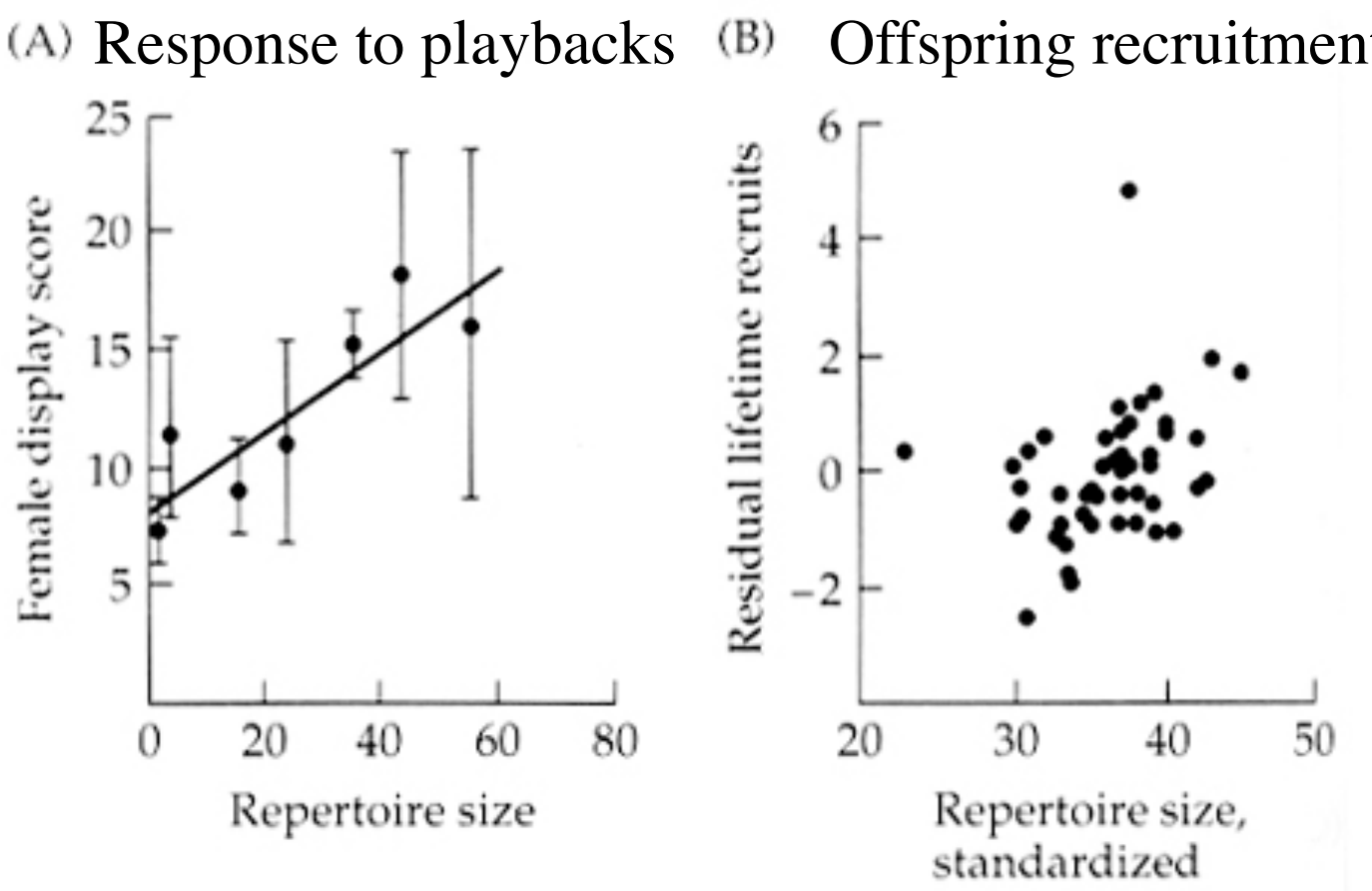
Effect of spots on offspring survival

32 Ornaments and good genes. Peacocks with more eyespots on their tails produced offspring that survived better when released from captivity into an English woodland park. *Source: Petrie [924].*

PETRIE M 1991 PEAHENS PREFER PEACOCKS WITH ELABORATE TRAINS
ANIMAL BEHAVIOUR 41: 323-331.

Takahashi M, Arita H, Hiraiwa-Hasegawa M, et al. 2008 Peahens do not prefer peacocks with more elaborate trains
ANIMAL BEHAVIOUR 75: 1209-1219.

Female preference for repertoire size in *Acrocephalus* warblers



Repertoire size may reveal condition during early development when males learn songs

Good genes and female choice

- But, meta-analysis revealed that only 1.5% of the variation in viability is explained by preferred male traits (Moller & Alatalo 1999)
- Sexual selection can accelerate loss of deleterious mutations, according to theory (Whitlock 2009) and data (Hollis and Houle 2009)
- More studies are needed that link mate choice to known genetic variation in viability

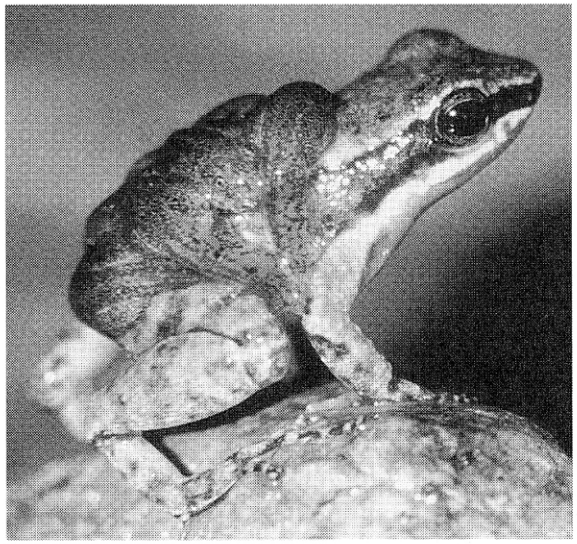
Moller AP, Alatalo RV 1999 Good-genes effects in sexual selection. PROCEEDINGS OF THE ROYAL SOCIETY OF LONDON SERIES B-BIOLOGICAL SCIENCES 266: 85-91.

Post-copulation calls

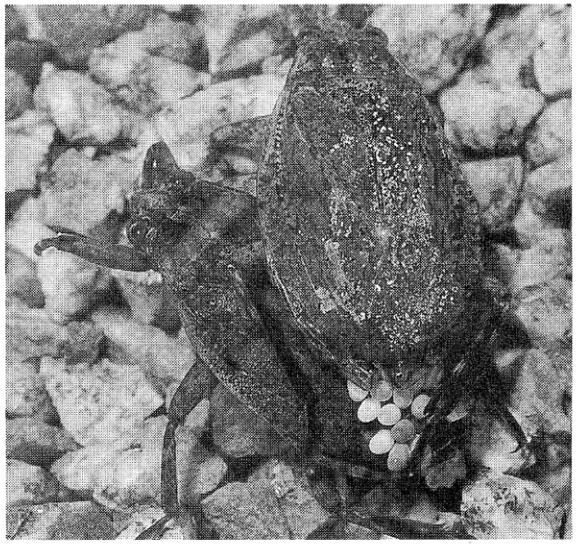
- Unique vocalizations given by males and/or females
- Function is unclear, several hypotheses exist:
  - Orgasm synchrony (humans and gibbons)
  - Subordinate females may use them to increase rank by soliciting future support from male (baboons)
  - Recruit additional mates and elicit male-male competition in elephant seals
  - Honest advertisement of male quality in rhesus monkeys since calling males are often attacked
  - Advertise mate guarding (male rat ultrasound)

Sex-role reversal

(A)



(B)



(C)

(D)