Territory signals

- Terms and definitions
- Game theory approaches to territory signals
- Assessment of neighbors
- Territory signal design rules
- Reading: pp 592-597, ch. 22

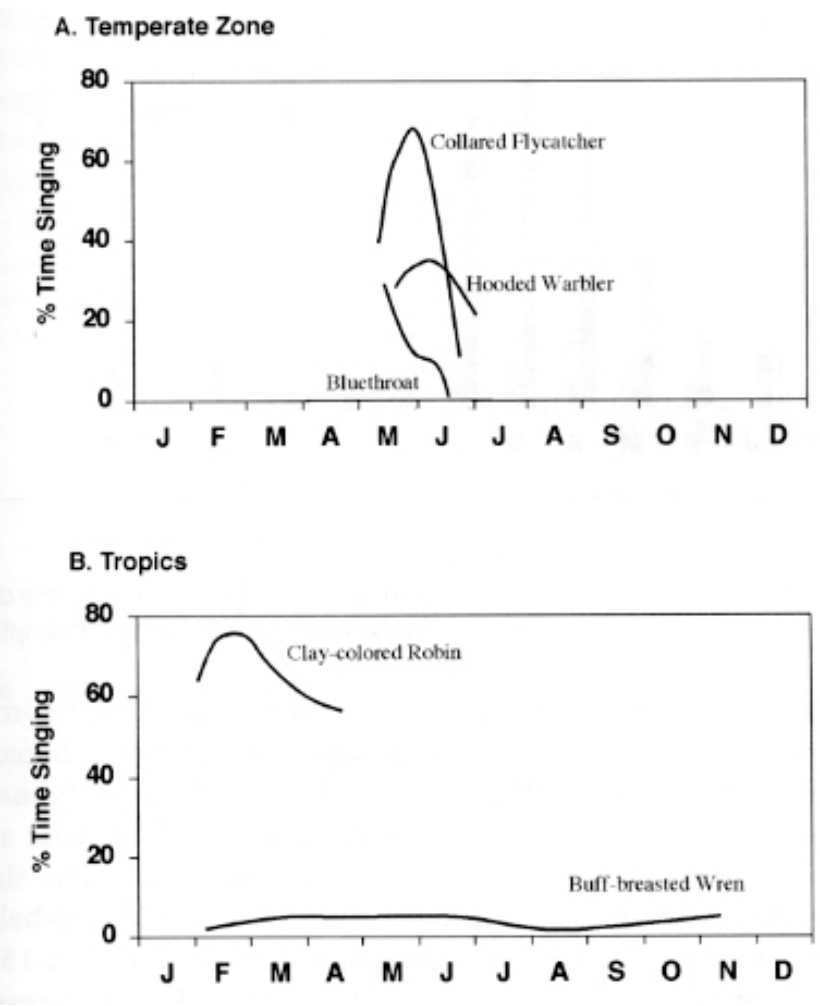
What is a territory?

- Territory: a fixed area from which intruders are excluded by an owner using advertisement, threat, and attack
- Types of territories
  - Breeding territory- small, contains only nesting or mating sites
  - Feeding territory-larger, support territory holder
  - All-purpose territory- largest, nesting site plus food for owner
  - Neighborhoods- networks of contiguous territories
- Territorial signal: a type of long-distance threat signal

Avian territoriality: temperate vs tropical

Temperate	Tropical
Highly seasonal	Year-round
Male only	Joint defense by pair or group
Male song	Female song, duets, and choruses

Stutchbury & Morton 2001

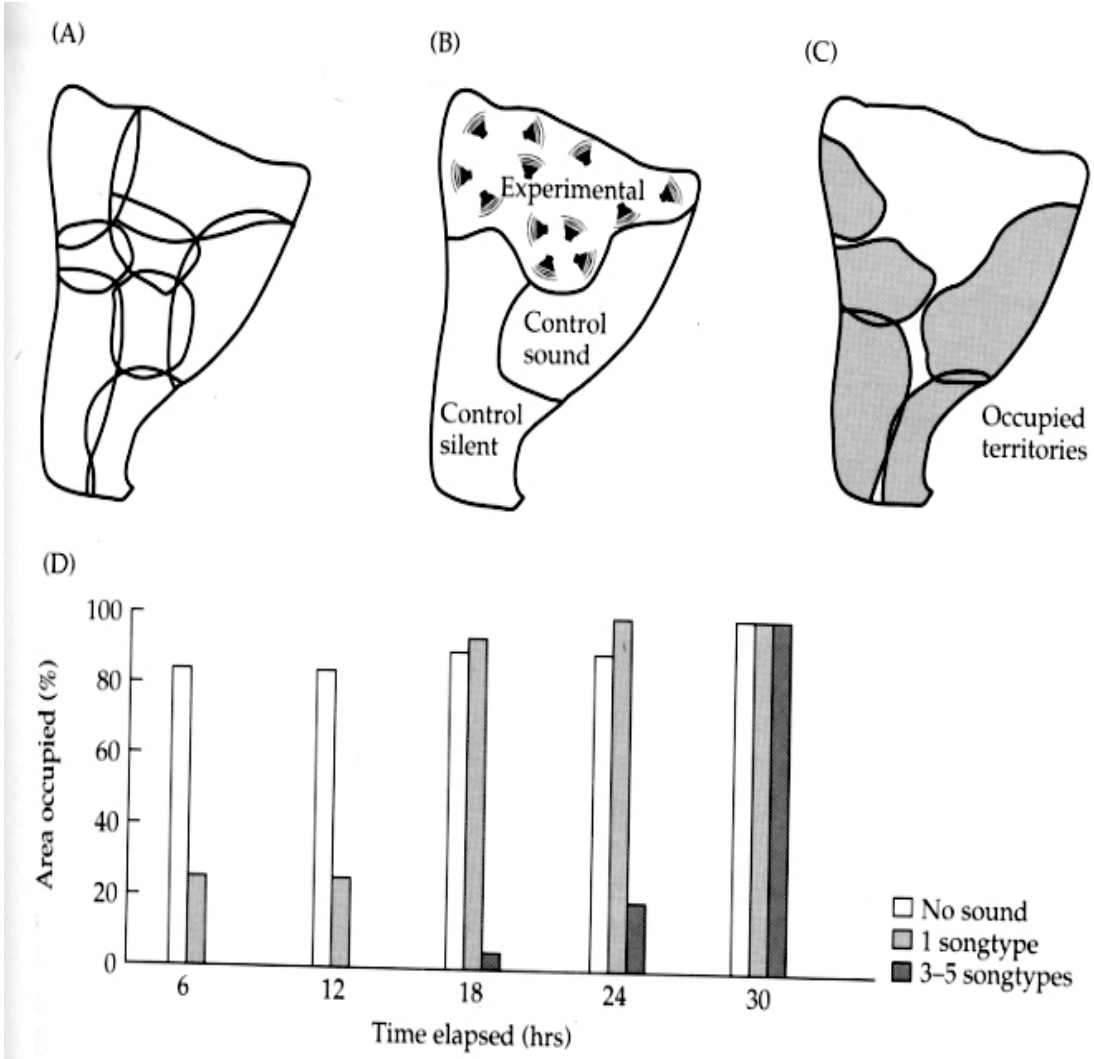


Keep in mind that not all territories are short-term

What effect do territorial signals have?

Great tit song

- Experimentally removed all owners
- Placed speakers with three treatments:
  - -no song
  - -single song type
  - -multiple song types
- New owners were less likely to settle where multiple songs were played



Ownership convention

- Territory owners tend to win encounters with intruders
  - neighborhoods often have stable membership and boundaries

Why?

- Arbitrary convention: owner always wins
- Asymmetry in fighting ability
- Asymmetry in valuation of territory

Uncorrelated asymmetry

- Opponents differ, but not with regard to fighting ability
- Example: hawk - dove - bourgeois
  - Bourgeois strategy: if owner play hawk, if intruder play dove
  - Assume that owner and intruder are equally frequent and get equal payoffs

	Opponent:	Hawk	Dove	Bourgeois
Actor:	Hawk	(V-C)/2	V	
	Dove	0	V/2	
	Bourgeois			

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	Opponent:	Hawk	Dove	Bourgeois
Actor:	Hawk	(V-C)/2	V	0.5H:H + 0.5H:D
	Dove	0	V/2	0.5D:H + 0.5D:D
	Bourgeois	0.5H:H + 0.5D:H	0.5H:D + 0.5D:D	0.5H:D + 0.5D:H

Uncorrelated asymmetry

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- Example: hawk - dove - bourgeois
  - Bourgeois strategy: if owner play hawk, if intruder play dove
  - Assume that owner and intruder are equally frequent and get equal payoffs:

	Opponent:	Hawk	Dove	Bourgeois
Actor:	Hawk	(V-C)/2	V	3V/4-C/4
	Dove	0	V/2	V/4
	Bourgeois	(V-C)/4	3V/4	V/2

Hawk-Dove-Bourgeois

If $V > C$ ($V = 2, C = 1$), then H is pure ESS

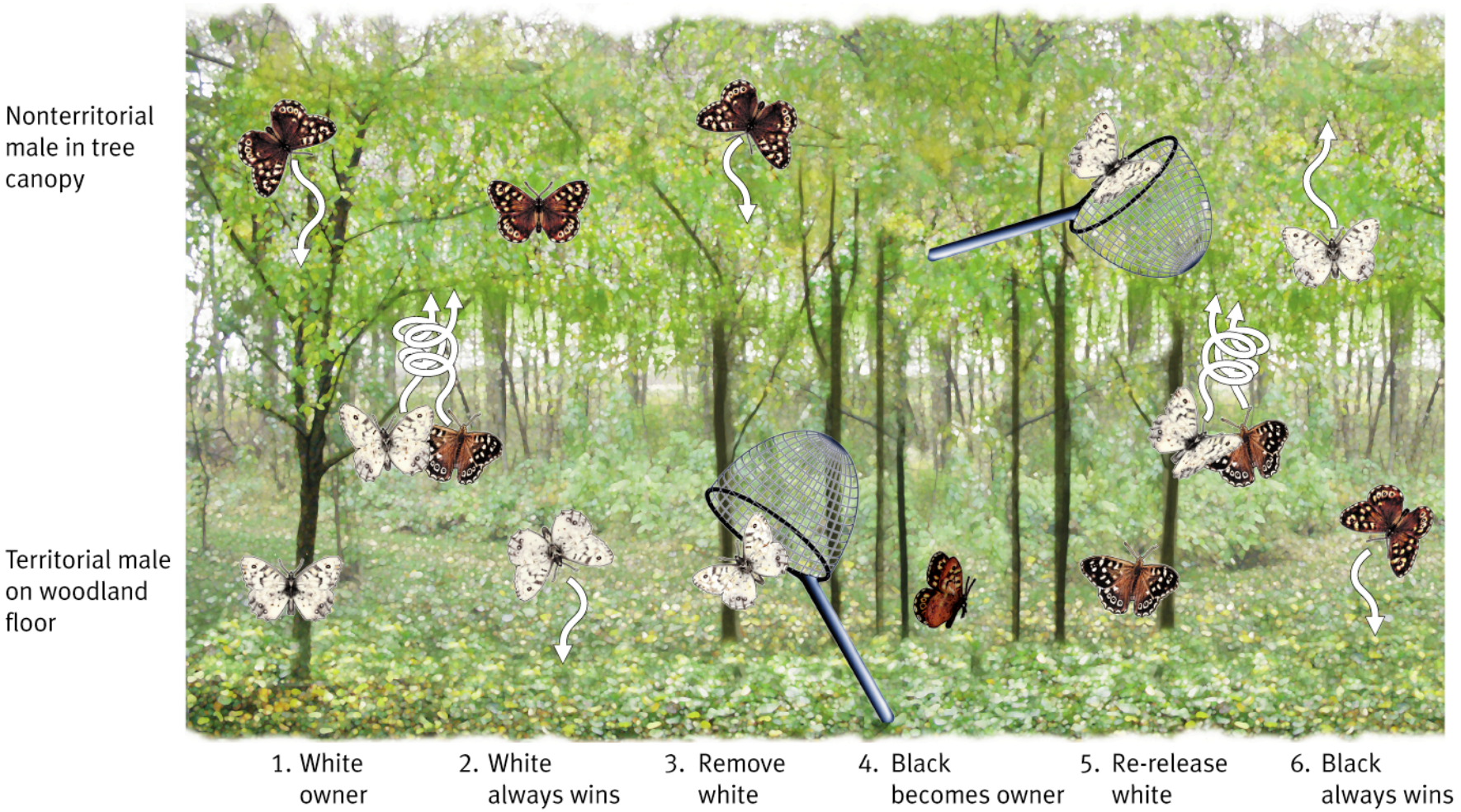
	Opponent:	Hawk	Dove	Bourgeois
Actor:	Hawk	1/2	2	5/4
	Dove	0	1	1/2
	Bourgeois	1/4	3/2	1

If $V < C$ ($V = 1, C = 2$), then B is pure ESS

	Opponent:	Hawk	Dove	Bourgeois
Actor:	Hawk	-1/2	1	1/4
	Dove	0	1/2	1/4
	Bourgeois	-1/4	3/4	1/2

Therefore, ownership alone may resolve conflicts when territory has low value

Residency in speckled wood butterflies



Do simple ownership conventions exist?

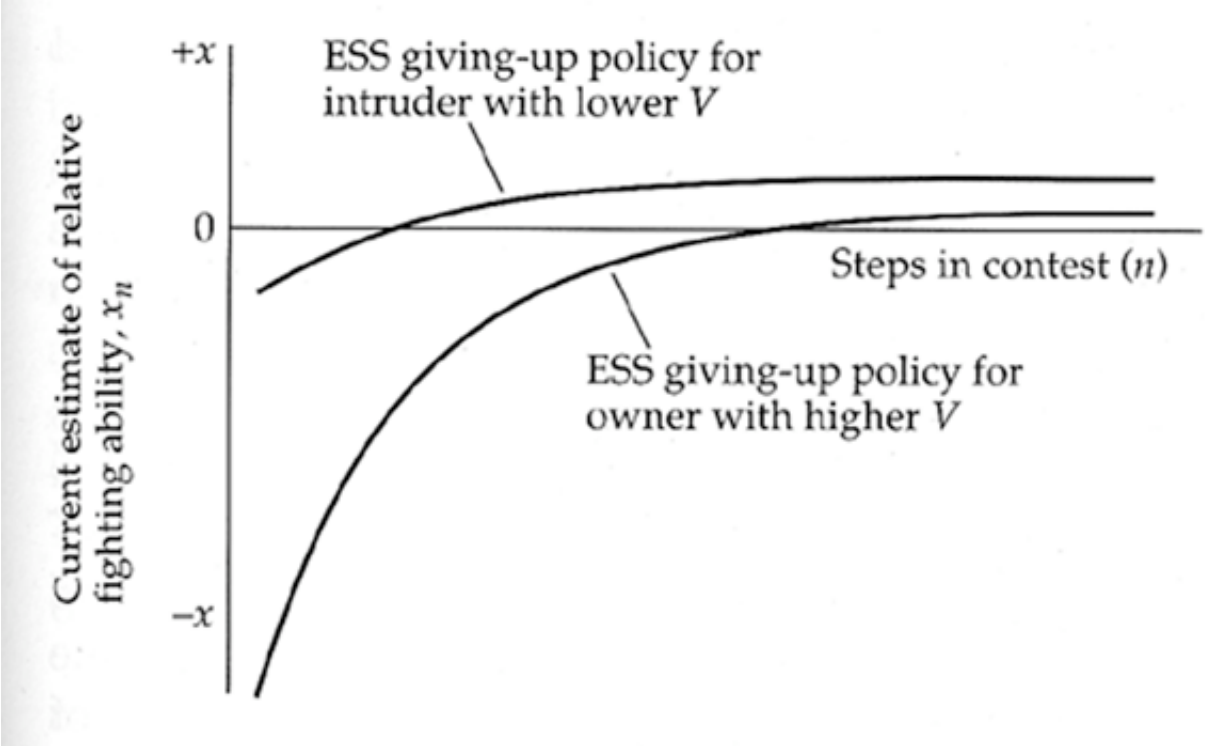
- Bourgeois convention for Speckled wood butterflies in England (Davies, 1978)
  - Males defend sunspots to attract females
  - Sunspots provide warmth for high activity levels
  - Owners contest with intruders using spiral flight
  - New owners always beat former owners after experimental removal
  - Territory value low because of ephemeral nature of territories?
- No bourgeois convention found in Sweden (Wickman & Wicklund 1983)
  - Returning owners engaged in long battles and usually won
  - differences in territory value or changes in fighting ability during removal?
- Territorial behavior depends on the body temperature of the resident (Stutt and Wilmer 1998)

Alternatives to ownership convention

- Owners differ from intruders in either relative fighting ability or valuation of territory
- Three territory games explore effect of asymmetries in fighting ability and territory value
  - Asymmetric hawk-dove (small owner has different payoffs than large intruder)
  - Asymmetric war of attrition
  - Sequential assessment
- All three games make similar predictions

Sequential assessment with owner-intruder asymmetries

- V = territory value, higher for owner
- k = fighting costs, assessed during contests
- V/k ratios differ for owners and intruders, set height of giving-up lines



Predictions:

- When fighting abilities are similar, owners should win because of higher V
- Duration should be longer if both contestants consider themselves owners
- In general, varying territory value has a stronger effect on ESS levels than varying fighting ability

Conclusions from territory games

- Simple conventions like ‘owner always wins’ are unlikely
- Territory valuation is often more important than fighting ability
- Territory owners value territories more than intruders because
  - Investment in reproduction
  - Increased probability of additional mates
  - Increased knowledge of food and hiding places
  - Stable boundaries with neighbors
- Territory signals should be designed to
  - Primarily convey value placed on territory (motivation to fight)
  - Secondarily convey fighting ability

Territory value depends on intruder type

- Owners - hold territory
  - high value to territory because of fitness benefits to be gained and high costs to losing territory
- Neighbors - defend other territory in neighborhood
  - low value to gaining a second territory relative to cost of defending two territories
  - Likely to have similar fighting ability to owner
- Floaters - do not hold a territory
  - high value to territory because low cost of losing and high benefit to winning
  - May have low fighting ability compared to owner

Neighbors as ‘dear enemies’

- Owners observed response to neighbors
  - Encounters initially aggressive
  - Settle to stable associations with repeated low-level encounters
  - Escalated response only necessary when neighbor trespasses
- Owners observed response to floaters
  - immediate escalation if observed on territory
- Termed the ‘dear enemy’ phenomenon
  - Observed during natural territorial intrusions
  - Also playback experiments at territorial boundaries versus inside boundaries
- Consistent with game theory predictions based on different relative V/k ratios

Neighbor versus floater intrusions

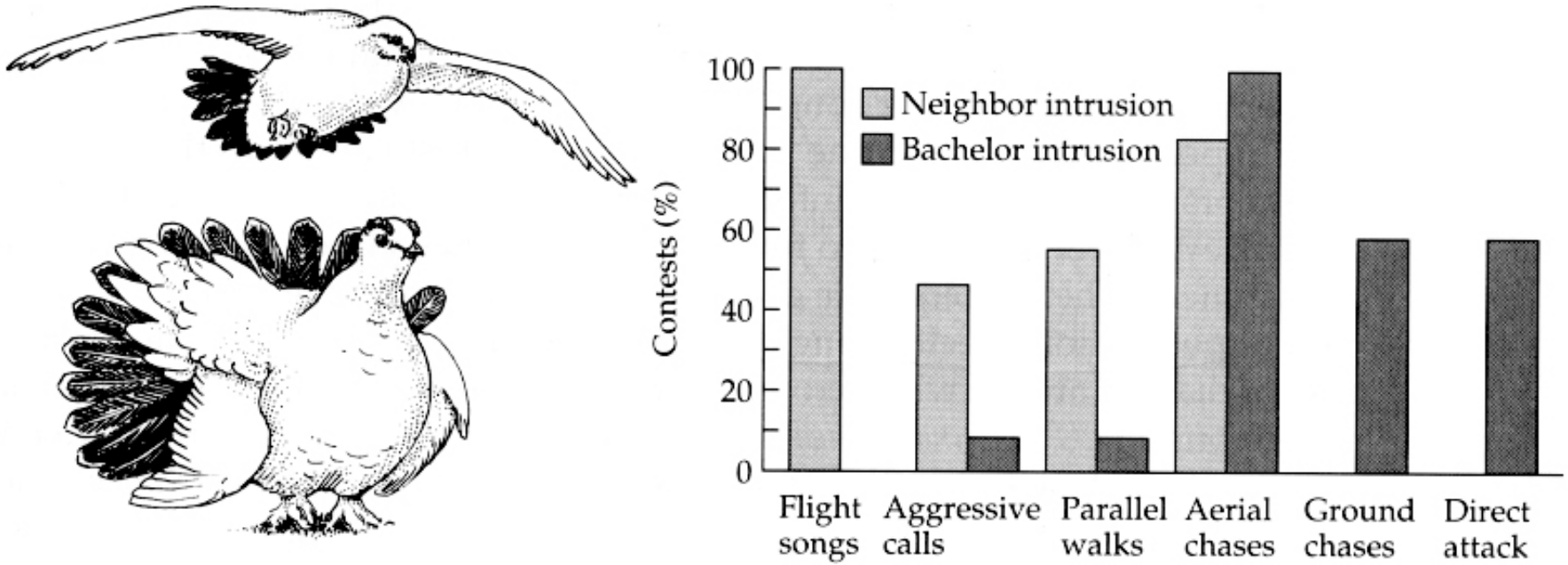
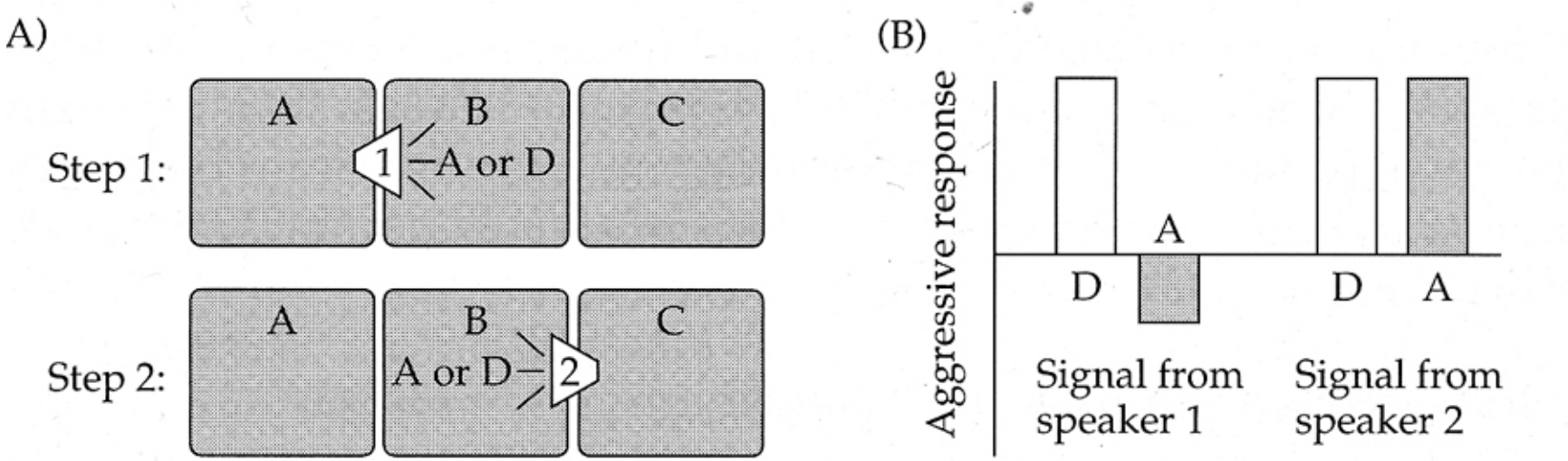


Figure 22.10 The frequency of behaviors performed in territorial conflicts in rock ptarmigan (*Lagopus mutus*). Black bars show the frequency of different behaviors used in interactions with intruding neighbors, and white bars show behaviors used in interactions with intruding bachelor floaters. Displays are clearly more frequent in neighbor interactions, whereas aggressive acts characterize bachelor interactions. (From Brodsky and Montgomerie 1987, © Springer–Verlag.)

Assessment of neighbors versus floaters

- Neighbors and floaters differ in threat to owners
- Owners need to be able to assess these differences
- Territory signalling expectations:
  - Ability to produce individually distinctive signals
  - Ability to discriminate among signals
  - Ability to memorize the location of neighbors

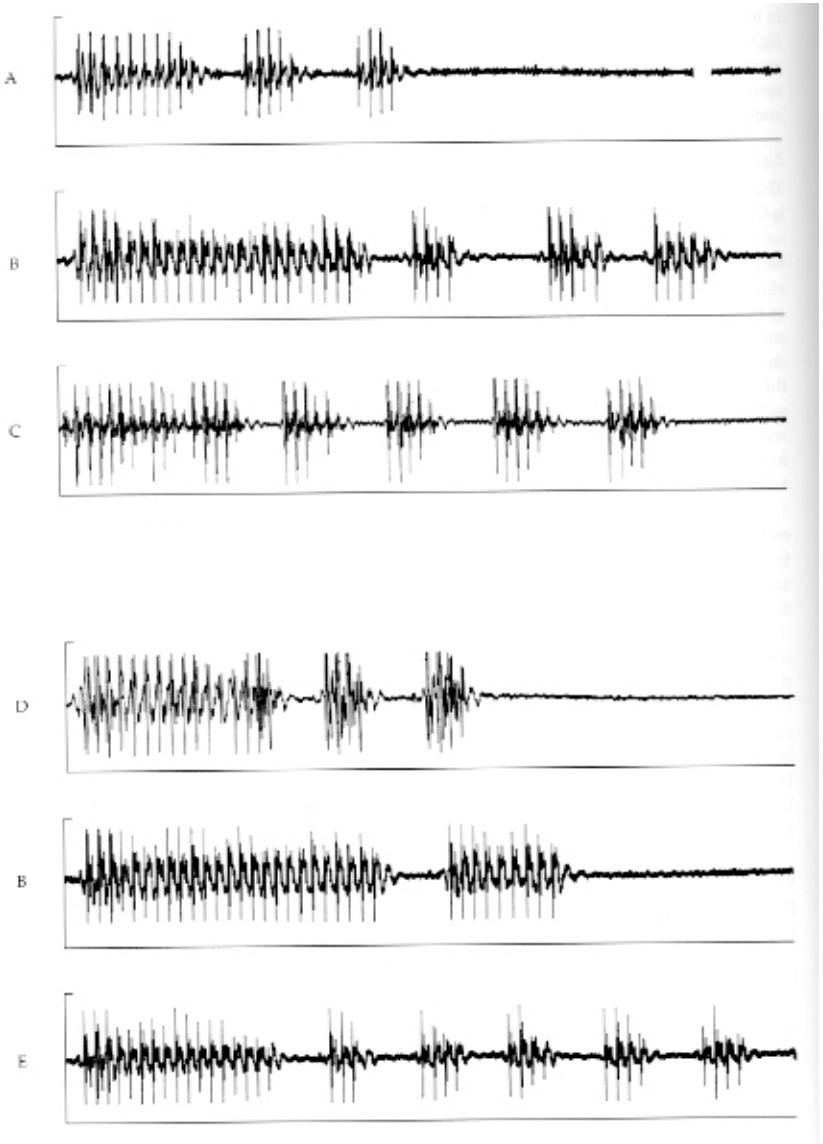
Neighbor-stranger discrimination



- Neighbor's song ignored when broadcast from proper territory
- Aggressive response when neighbor's song broadcast from different territory
- Rule of thumb: recognize neighbor when in own territory, treat all other songs as if from floaters

Individual signatures in kangaroo rats

- Individually distinctive temporal patterns of hindfoot drumming
- Signatures change when individuals move to new territories
- Signatures shifted to make them maximally distinctive from neighbors

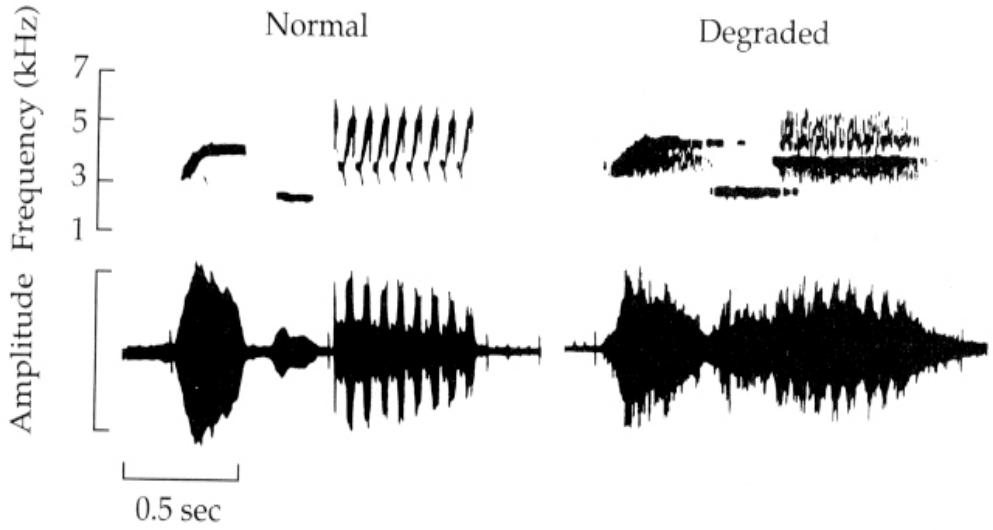


Randall 1995 AnimBehav. 49:1227-1237

Sound degradation and ranging

Rufous-sided towhee

- Signal amplitude
- Frequency dependent attenuation
- Reverberation



- Owners benefit from knowing distance to singing neighbor
  - Avoid wasting energy in investigating
  - Avoid unnecessary fights with neighbors
- The ranging hypothesis (Morton 1982)

Examples of ranging

- Playbacks of song in territories of Carolina wrens (Morton 1986)
  - Respond to undegraded song by approaching loudspeaker
  - Respond to degraded song by singing at a distance
- Playbacks of song to Kentucky warblers (Wiley & Goddard 1996)
  - Fly directly to speaker playing undegraded song
  - Fly past a speaker playing degraded song

Competition in territorial signals

- Variation in singing strategies
- Song matching
- Song dialects

Singing strategies in territorial songbirds

Table 22.1 A summary of the mean values of song variables for songbird species employing different types of singing strategies

	Singing Strategies			
Song variable	**One songtype**	**Bout**	**Mixed**	**Infinite[a]**
Size of songtype repertoire	1.0	8.1	20.2	∞
No. of syllable types per song	3.8	4.6	7.0	3–∞
Song duration (sec)	6.1	1.8	2.0	0.3–∞
Intersong interval (sec)	6.6	5.7	5.2	0–10.5
Duty cycle (%)	31	27	24	22–100
Song delivery rate (per min)	7.2	12.3	12.4	−∞–130.4
No. of species	24	34	28	15

Source: Based on data from Read and Weary 1992.

[a]Minimum and maximum values are given for infinite repertoire species.

Some singers have multiple songtypes in repertoires

-Mixed-mode singing = ABCDABCDABCD

-Bout signing = AAAABBBBCCCCCCDDDD

-Infinite = really big number of songtypes

Multiple songtypes: Why different repertoire sizes?

- Anti-habituation (receiver)
- Anti-exhaustion (sender)
- Beau Geste
  - Multiple songtypes deceive intruders
- Ranging
  - New songtypes make neighbor ranging more difficult
- Escalation by matching

Song matching reveals motivation

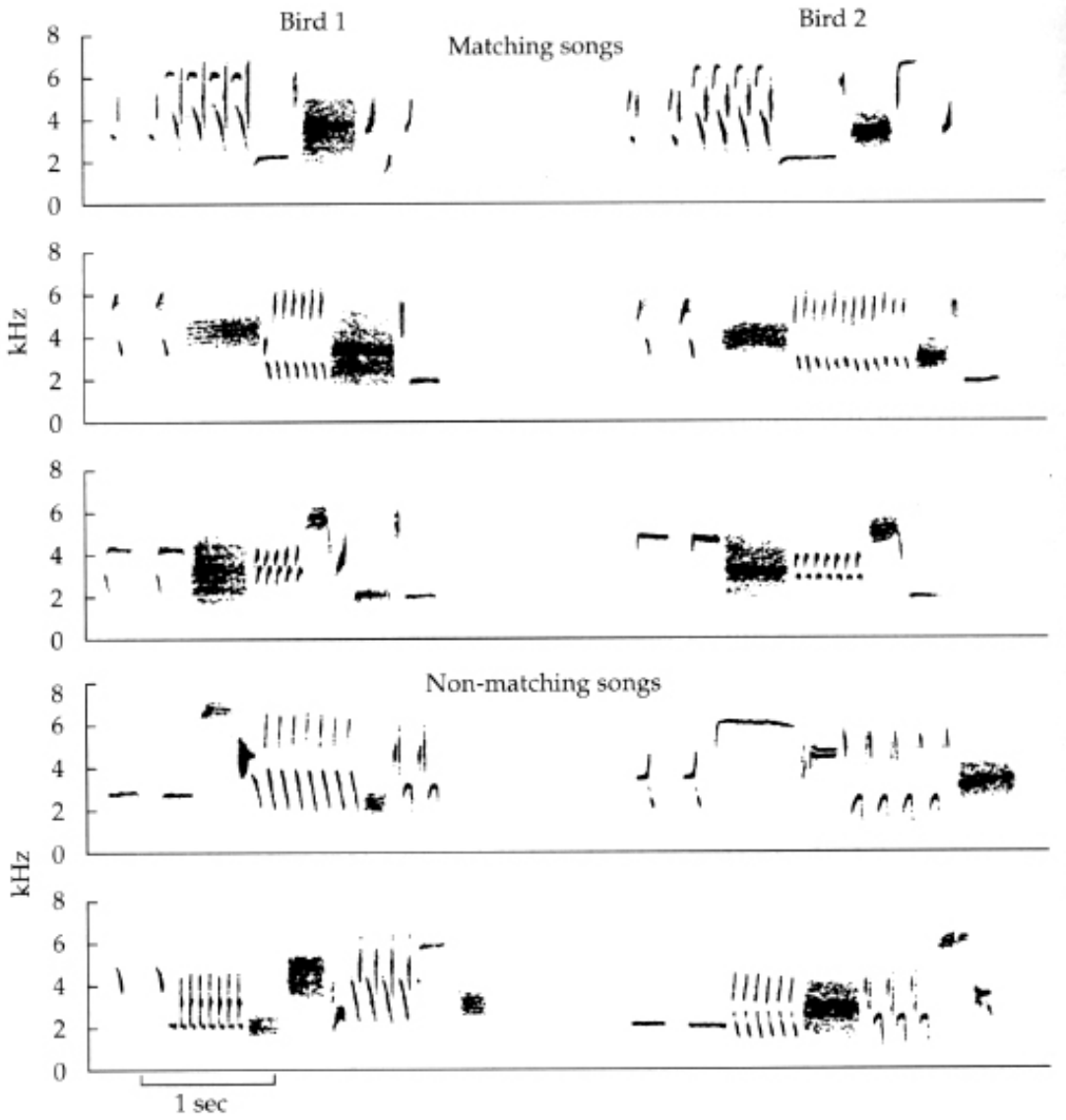
Song matching in song sparrows

Neighbors share some, but not all, songs in their repertoire

In contests, individuals can
-songtype match,
-repertoire match, or
- fail to match

Interactive playbacks show rate of singing, rate of songtype switching, and type of matching all indicate aggressive motivation

Intruders with larger repertoires who can match songtypes are more successful at gaining territories



Song dialects

Song dialects in white-crowned sparrows

•Song learning is used to match neighbor's song after juvenile settlement

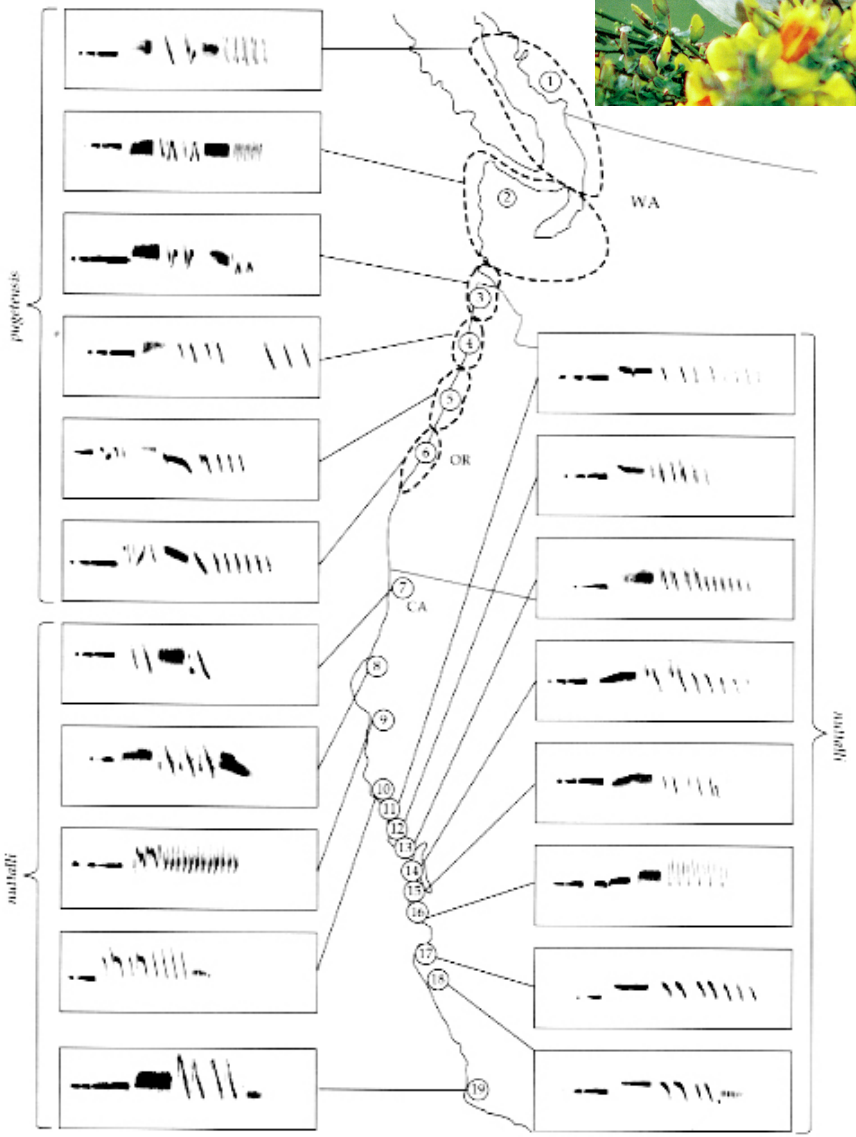
•Results in song 'dialects' and patchwork variation

• Matching neighbors' song appears to be important for obtaining territories

•Does not preclude individual recognition

•Dialects more common in stable environments like the tropics

- •Smaller dialects in sedentary populations of WCS
- •Larger, looser dialects in migratory populations

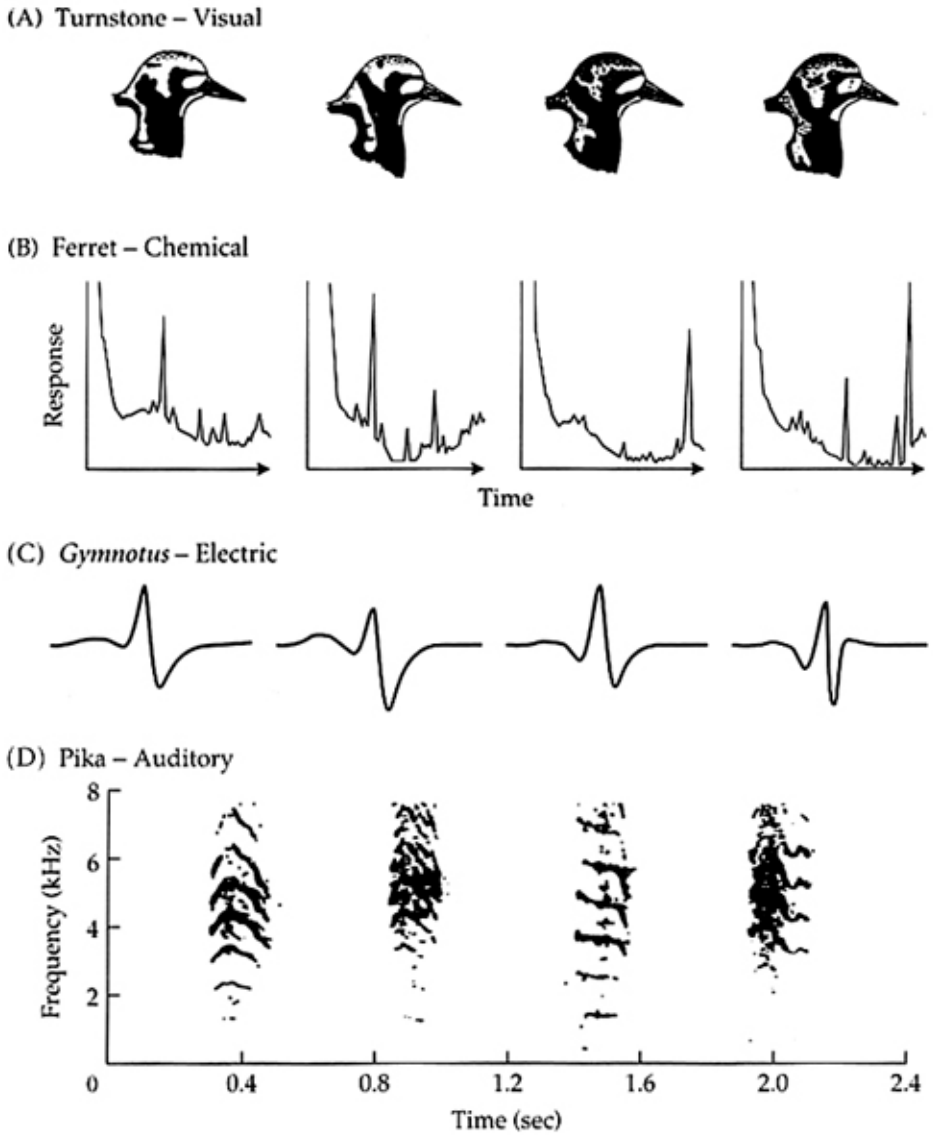


Territory defense signal design rules

Table 18.4 Design rules and modality-specific mechanisms for territory defense signals

Design feature	Rule	Visual mechanisms	Auditory mechanisms	Olfactory mechanisms
Range marks	Moderate (territory boundary)	Posture Color patch	Loud call	Deposited Low volatility chemical
Locat-ability	Territory and/or Owner	Presence on territory	Amplitude cues Degradation cues	Frequent marks along boundary Sender not locatable
Duty cycle	Variable	High when owner present	Long-duration signal Few repetitions per day	Long fadeout Embed in sebum Volatile when sniffed
ID level	Species Individual	Color pattern Presence on territory	Frequency Temporal pattern Note shape Syntax	Chemical mix
Modula-tion level	Some graded components	Coverable color patch	Repetition rate Song type variation	Add chemical related to dominance
Form-content linkage	Arbitrary	Exploit preexisting visual biases	Exploit preexisting sender production mechanisms	De novo production

Hierarchical information in territory signals



- Large-scale pattern identifies species
- Variation around mean identifies individuals

Territory marking in European badger

- Olfactory deposits are a mix of feces and an anal gland secretion

- 70% of marks deposited around boundaries of territories