# Conflict Resolution

- Threat signal design rules
- Threat-display contests
  - Hawk-dove-assessor
- Variable length contests
  - War-of-attrition
  - Sequential assessment
- Variable sequence contests
- Read pp 598-602, ch. 21

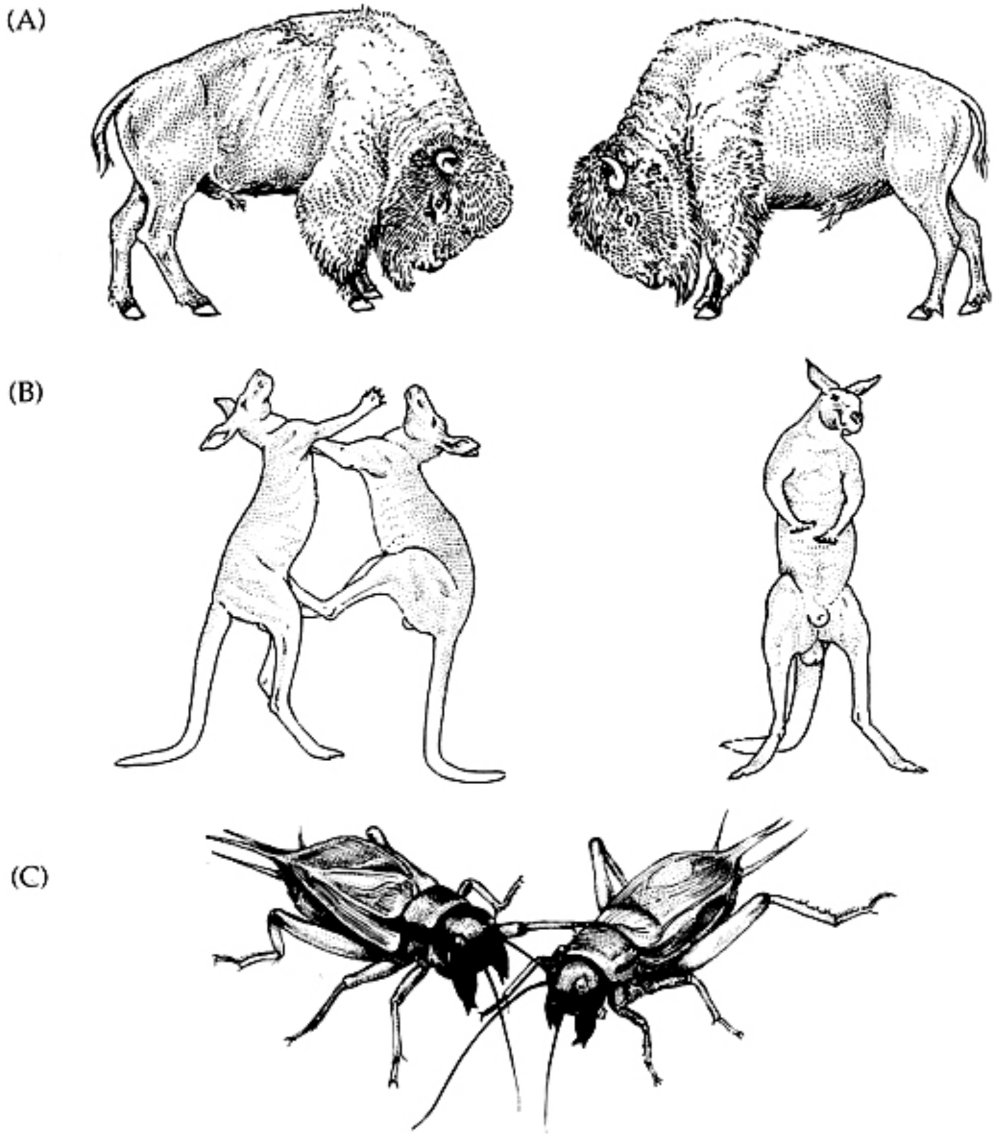
# Signal design rules

- Signal range
- Locatability
- Duty cycle
- Identification level
  - Requires variation between classes
- Modulation potential
  - May encode motivation, aggressiveness, health, danger
- Form-content linkage
  - Signal form depends on signal content in an arbitrary or linked way

# Threat signal design rules

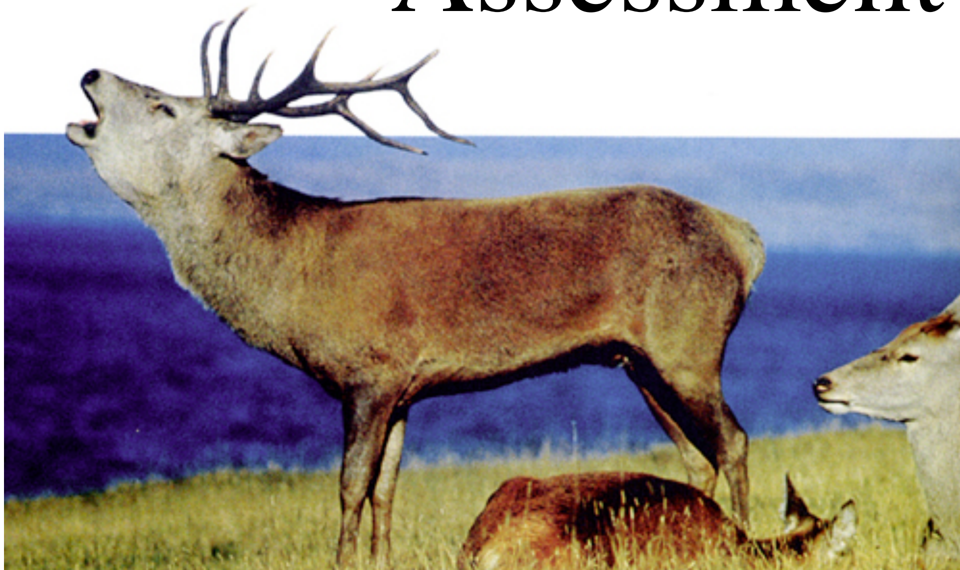
**Table 18.5** Design rules and modality-specific mechanisms for threat signals

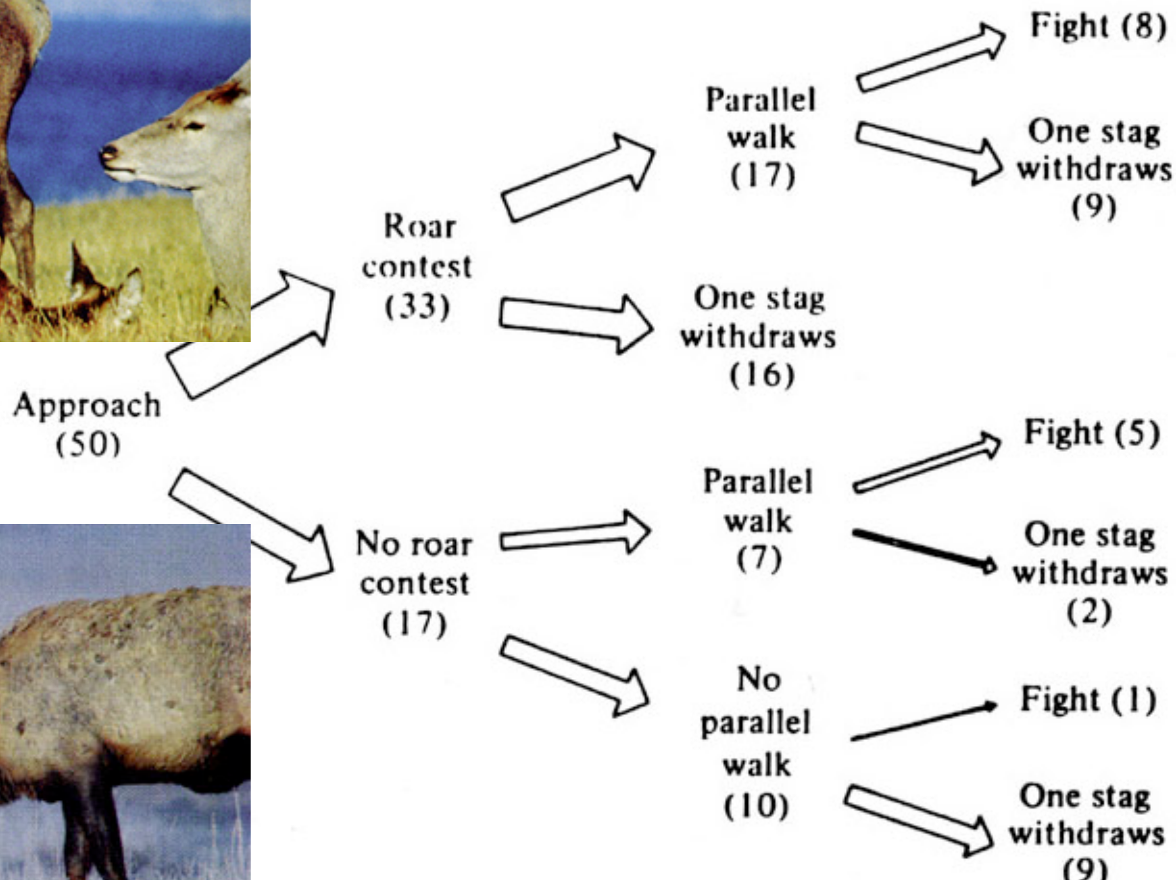
| Design feature | Rule | Visual mechanisms | Auditory mechanisms | Olfactory mechanisms |
|---|---|---|---|---|
| Range | Short | Posture<br>Movement display | Soft broadband growl<br>Loud scream | Volatile, rapid fadeout chemical |
| Locat-ability | Intended receiver (rival) | Directional display or posture | Beam sound<br>Countersinging | Directed flow<br>Add visual component |
| Duty cycle | High for contest duration,<br>Short signals | Series of single short displays | Series of single short calls<br>Longer single growl | Single puff |
| ID level | Rival class: Age, body size, status | Maturational color change<br>Broadside display<br>Badge | Frequency shift with age or body size<br>Intensity | Chemical derived from maturation hormone |
| Modula-tion level | Graded | Variable position or display form<br>Choice of display | Frequency<br>Intensity<br>Repetition rate | Poor |
| Form-content linkage | Linked | Attack or retreat intentions<br>Body size amplifier | Lowest possible frequency<br>Wide bandwidth | Testosterone-derived chemical |




Conflict displays often involve intention movements

# Assessment in red deer





# Correlated asymmetry

- Opponents differ in size or other measure of RHP
- Example: hawk - dove - assessor
  - Assessor strategy: if larger play hawk, if smaller play dove
  - Assume 50% population is larger, 50% smaller than actor

| Actor \ Opponent: | Hawk | Dove | Assessor |
|---|---|---|---|
| Hawk | (V-C)/2 | V | (V-C)/2 |
| Dove | 0 | V/2 | V/4 |
| Assessor | V/2 | 3V/4 | V/2 |

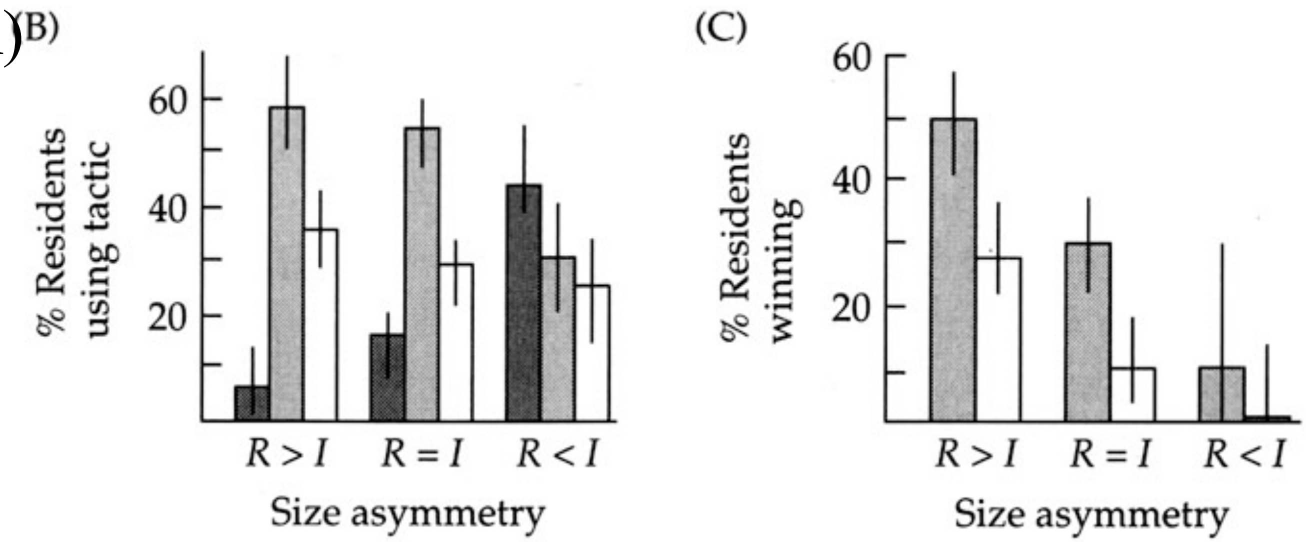
When there is a cost to fighting, Assessor is pure ESS
assuming that assessment is cost free and accurate

# Assess and bluff by mantis shrimp

Threat display. Newly molted animals can be severely injured. Up to 20% of animals on a reef are vulnerable.

Responses of newly molted residents (R) & intruders (I):

Dark-flee
Grey-display
Open-do nothing



# War of attrition - the waiting game

- Assumptions
  - Resource cannot be shared
  - Cost of display increases with length of contest
  - No information is received during contest and opponents are symmetrical
  - Each contestant makes a "sealed bid" for how long they are willing to persist
  - Winner will be the contestant willing to persist longer and accept the higher cost
  - The cost to both contestants equals the cost acceptable to the loser

# War of attrition - Payoff matrix

$x_i$ = amount of time individual i displays
k = rate at which costs are expended
V = value of resource

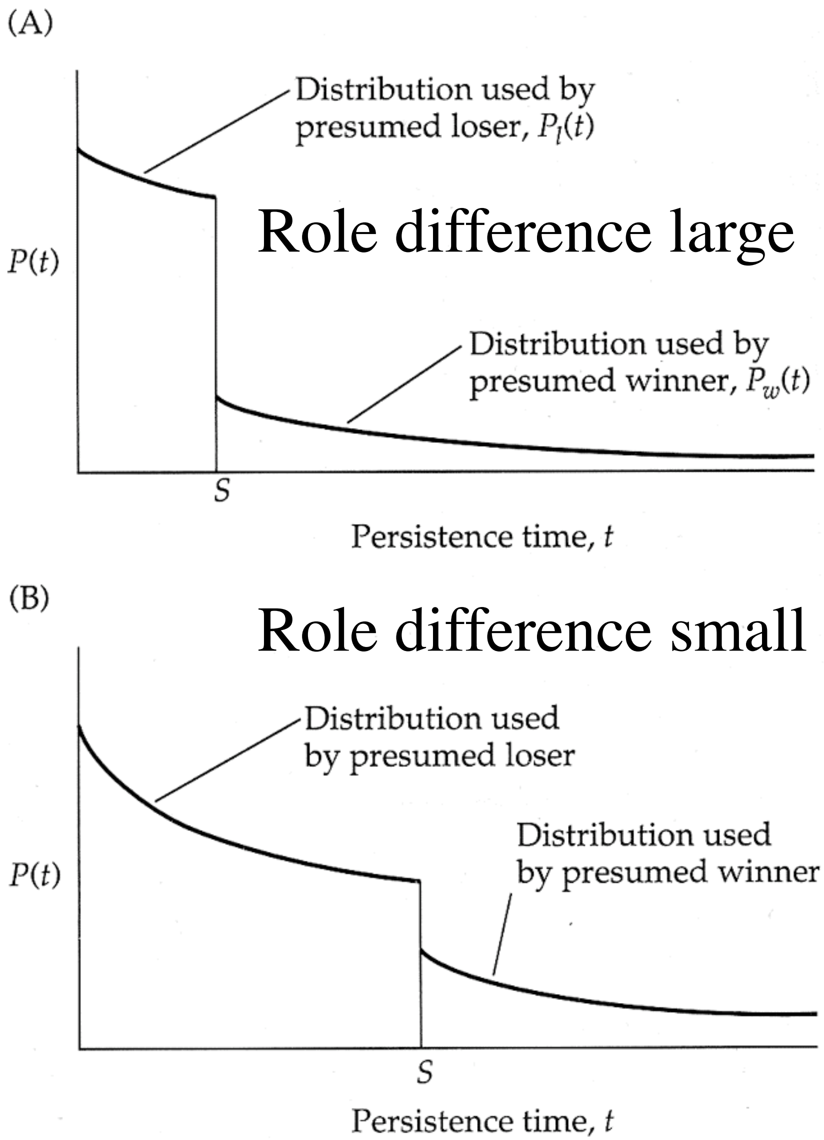
| Payoff to: | | Player A | Player B |
|---|---|---|---|
| Actor : | $x_A > x_B$ | $V - kx_B$ | $- kx_B$ |
| Opponent: | $x_A < x_B$ | $- kx_A$ | $V - kx_A$ |

No pure ESS is possible, since an opponent that displayed a little bit longer would have higher fitness
Solution is a mixed ESS where the probability of leaving at any time is a constant. The times an individual stays should be distributed as a negative exponential, more short than long.

# Asymmetric war-of-attrition

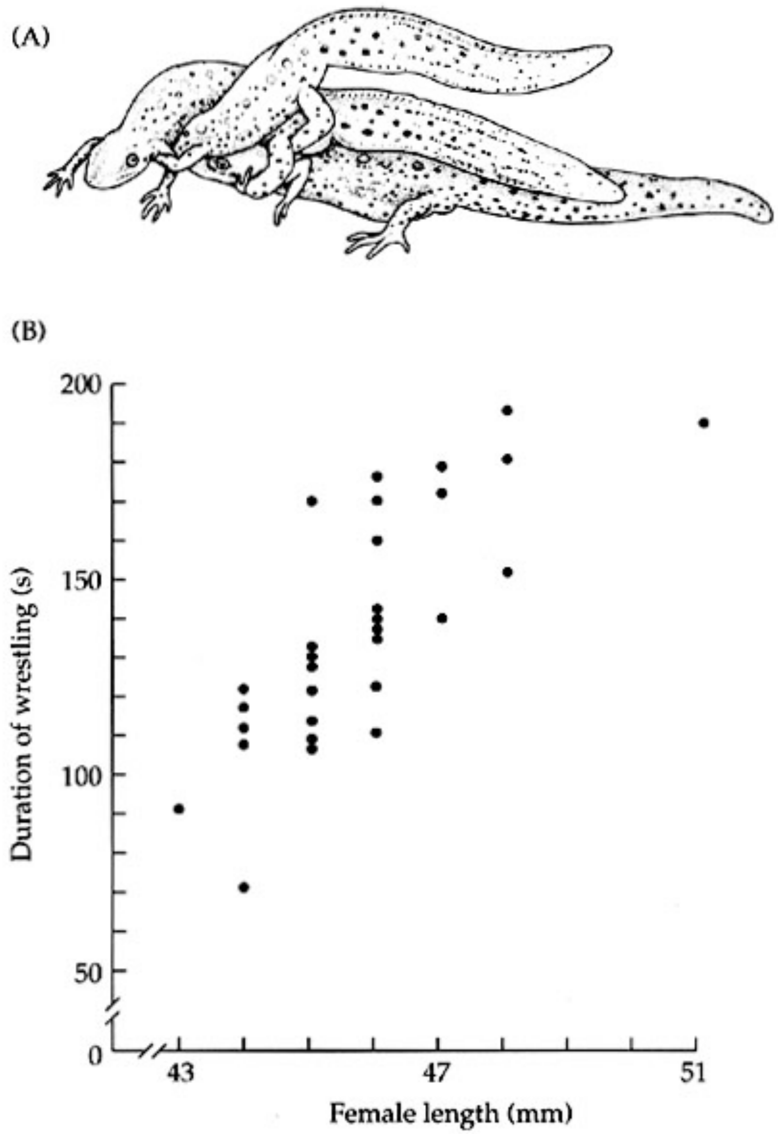
- If animals experience different costs of display or the resource differs in value to them, the game is asymmetric
- Which player has the largest V/k will win, but this may not be known
- This may lead to two different giving up time strategies

# War-of-attrition solutions




- ESS: Perceived winner and perceived loser select S (contest investment) from non-overlapping distributions
- Prediction 1: When V/k ratios are higher, contest duration increases
- Prediction 2: When V/k ratios are more similar, contest duration increases and variance in duration increases

# Fight duration and resource value in newts



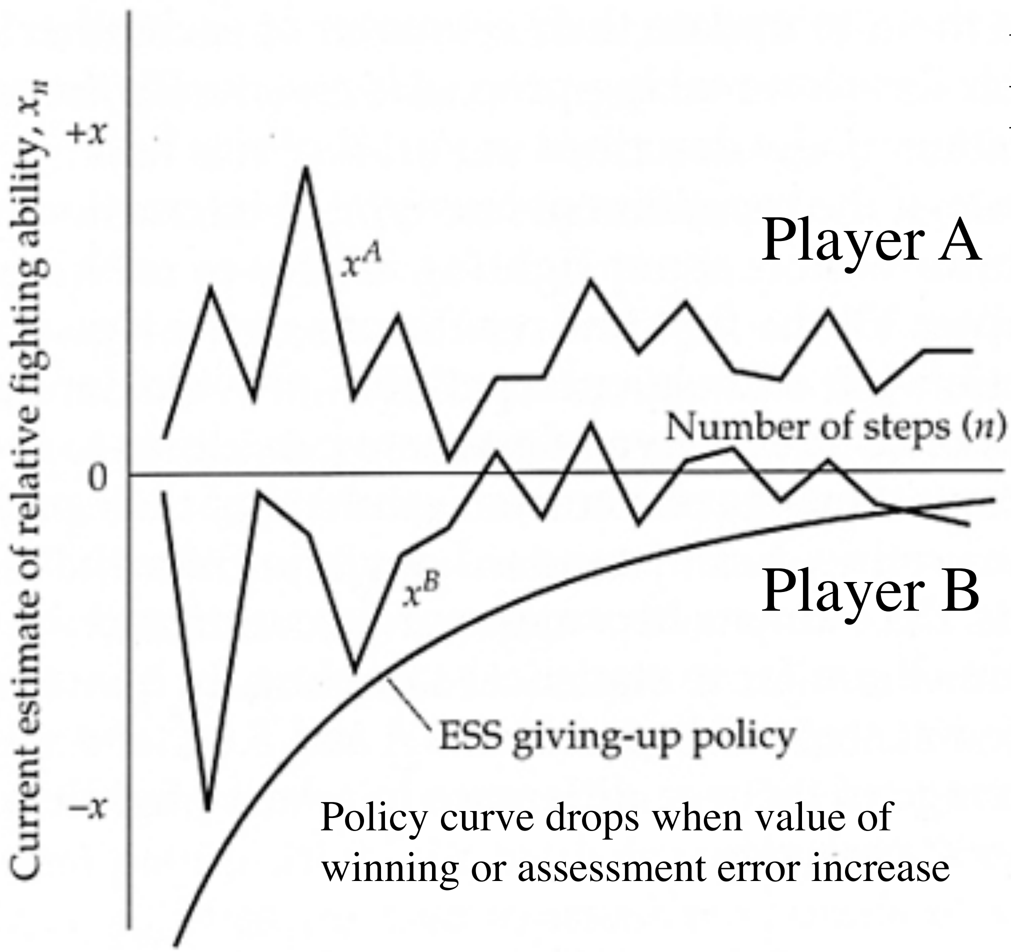

Larger females carry more eggs.

Males fight longer over larger females.

# Sequential assessment

- Assumptions
  - Animals display in order to acquire information about each other's fighting ability and resource value
  - Fights only occur when animals are closely matched
- Assessment may occur via a single repeated display, or a series of different displays
- Animals improve their estimate of relative fighting ability with each round of display
- The ESS is to end fight when your estimate of relative fighting ability drops below a "giving up line"

# Sequential assessment ESS




Dynamic programming model

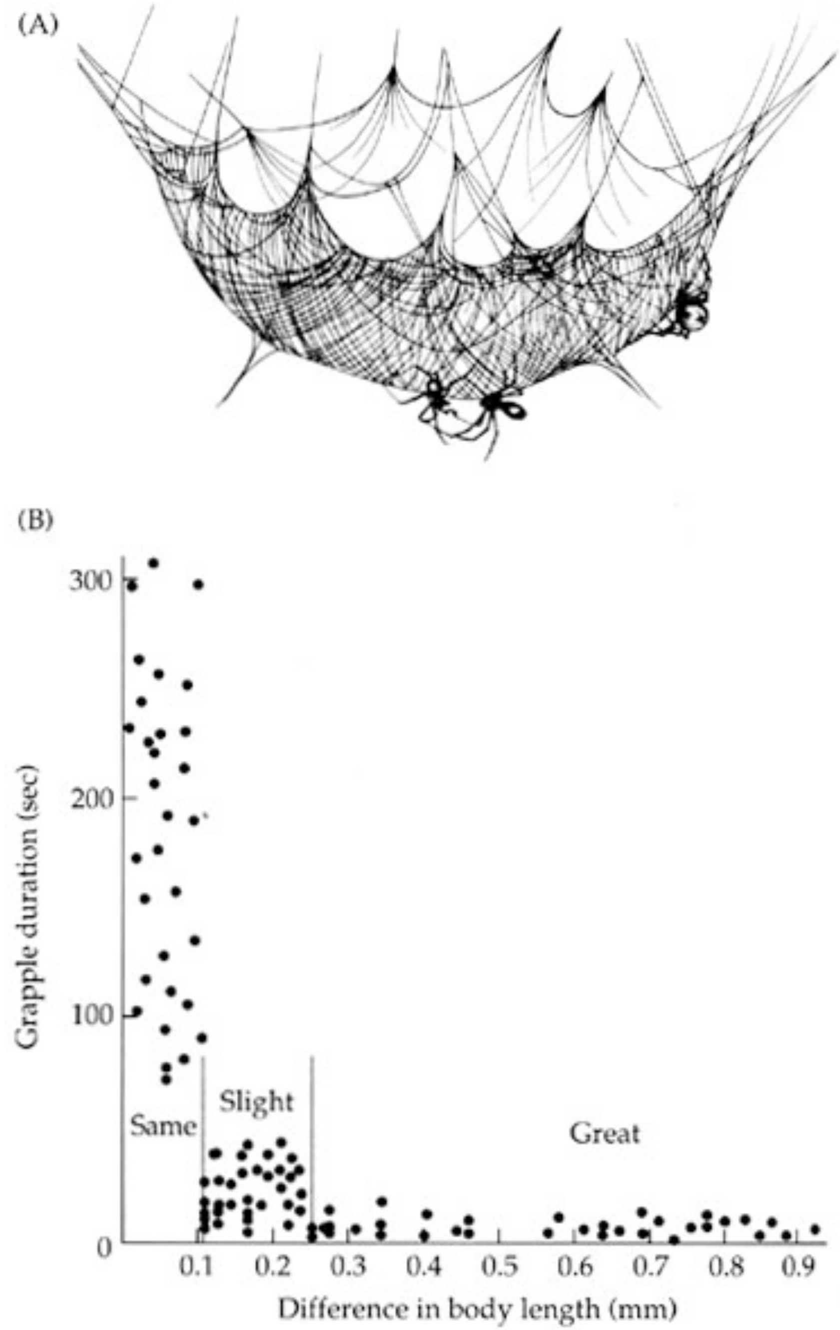
Predictions

- –Fight duration increases as the asymmetry in fighting ability decreases and/or as resource value increases
- –The cost of a fight increases as the asymmetry in fighting ability decreases
- –Probability of winning increases with asymmetry

# Contest duration and body size difference in doily-and-bowl spiders

- Males fight over access to females on webs

- Longer fights and higher variance in fight duration when body size of males more similar



# Ownership effects in spider fights

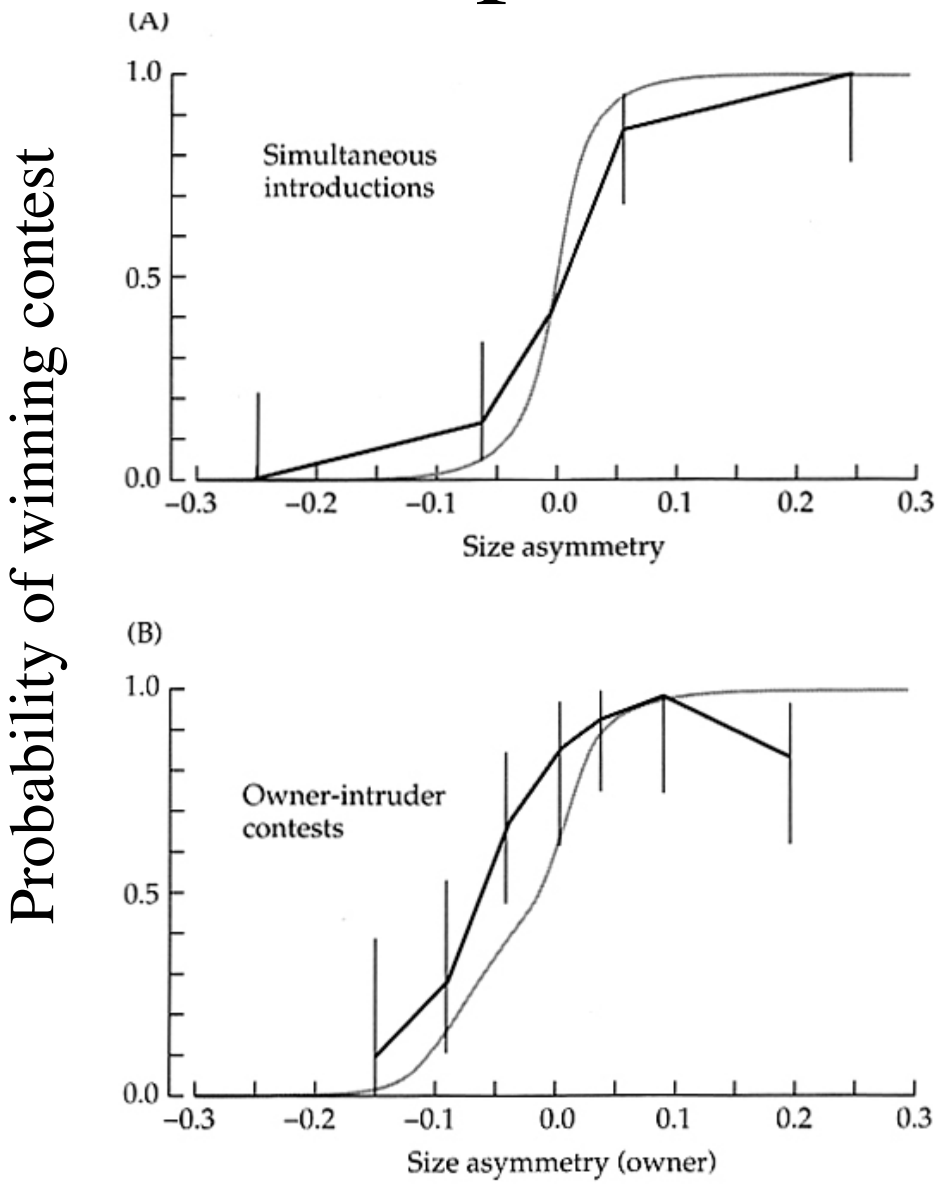



**Figure 21.9 Predicted and observed relationship between size asymmetry and probability of winning in the bowl and doily spider.** The dashed line shows the quantitative prediction from the sequential assessment game. The solid line with error bars shows the observed probability of winning. Size asymmetry is computed as the natural log of the ratio of the larger to the smaller contestant. (A) Simultaneously introduced males. There is a good fit between observed and predicted probabilities. (B) Owner-intruder contests. Given their size, owners have a higher probability of winning than expected when a female is present. (After Leimar et al. 1991.)

# Sequential assessment in phases

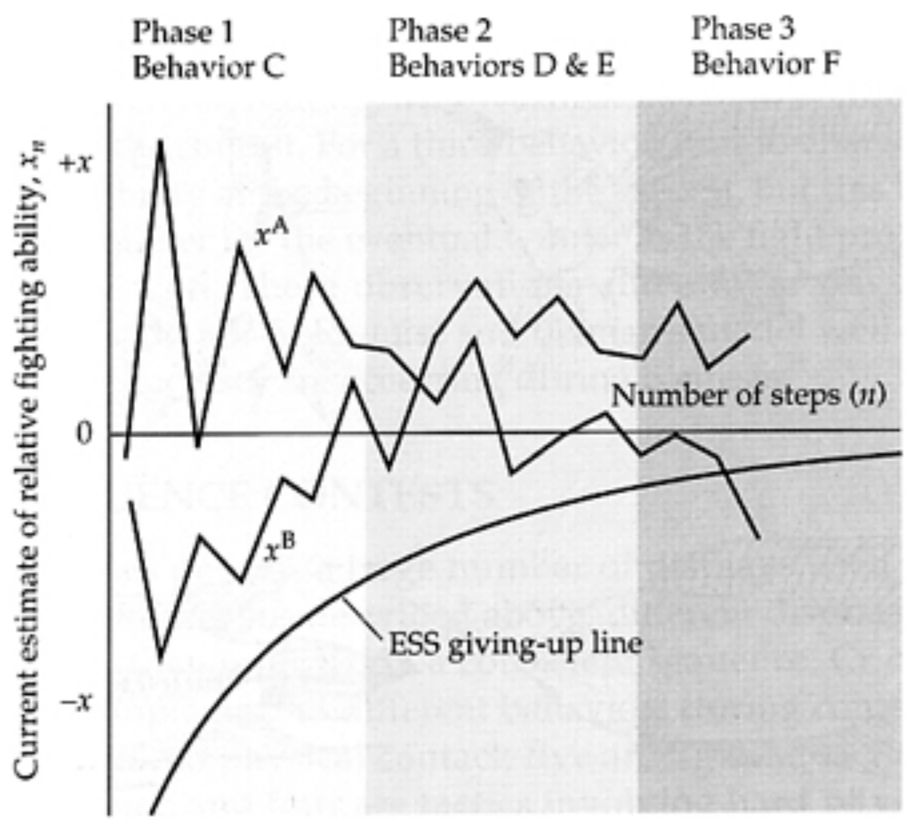
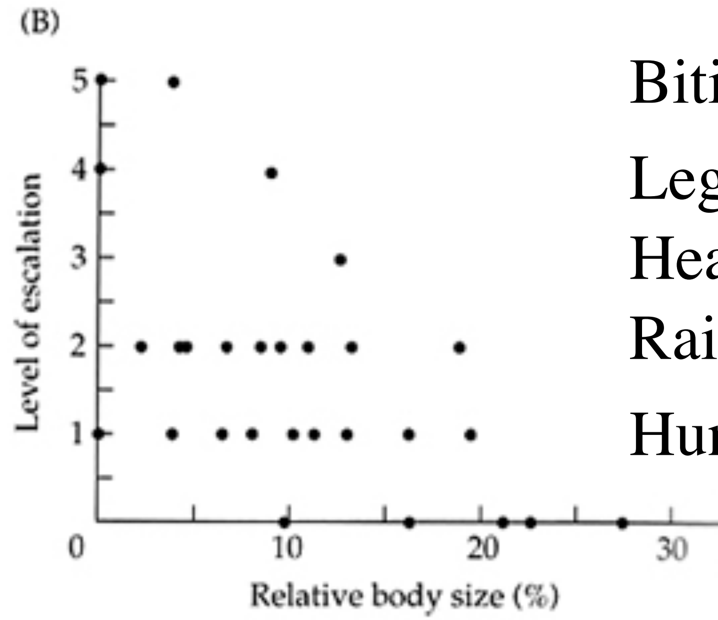



**Figure 21.11 The sequential assessment game with several different behaviors.** During the first stage, only behavior C is used; in the second stage, behaviors D and E are used; and in the final stage F (fighting) occurs. Axes are the same as in Figure 21.8. In this example, individual A gives up first. (After Enquist et al. 1990.)

# Jumping spider contest stages




Biting

Leg wrestle

Head butt

Raise legs

Hunch body

**Figure 21.10 Stages in jumping spider contests.** Contests in *Euophrys parvula* consist of distinct stages, always beginning with stage 1 and escalating to the next stage until one individual retreats. Each stage is associated with a different type of display or behavior, and each subsequent stage is associated with increasing risk of injury. All of the behaviors are mutual and performed by both spiders, i.e., when one escalates the other follows. (A) The stave display of stage 2. (B) The stage of escalation reached increases when the contestants are more similar in size. (A courtesy of Lyn Forster; B from Wells 1988.)

# Sequential assessment in cichlids

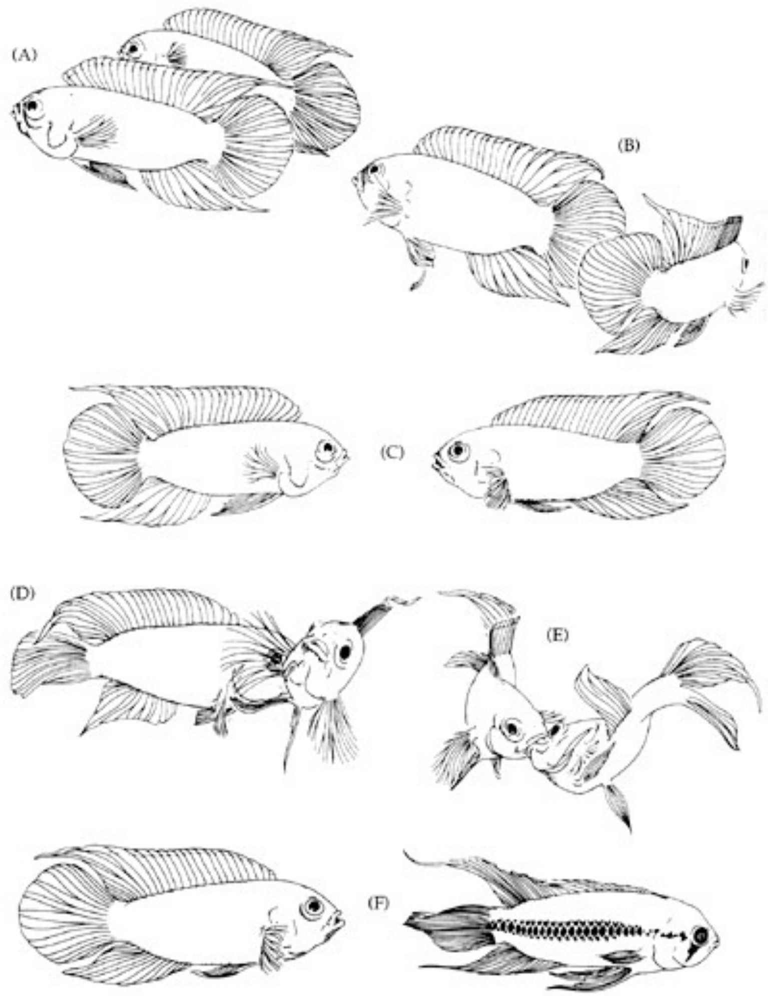
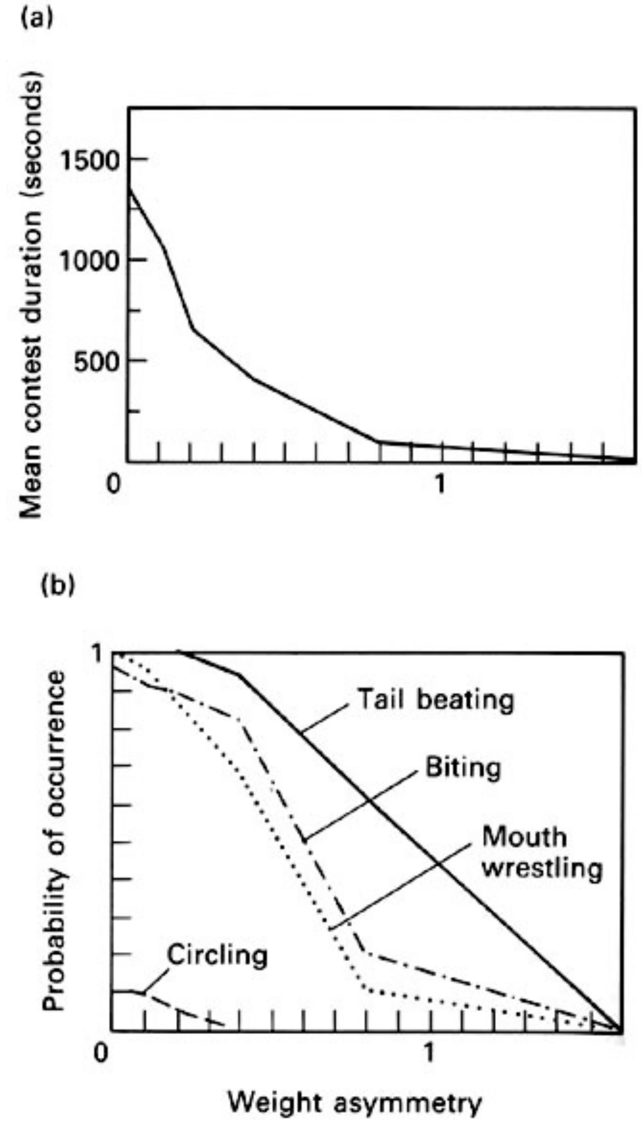



**Figure 21.12 Fighting sequence in the cichlid fish *Nannacara anomala.*** (A) Broadside display, (B) tail beating, (C) frontal orientation, (D) biting, (E) mouthwrestling, and (F) termination, in which the loser on the right adopts midline darkening and lowered fins. (From Krebs and Davies 1995, based on Jakobsson et al. 1979.)



# Why give multiple signals?

- Each display serves a different function
- Displays transmit graded information about display intentions
  - Multiple signals may lower potential risk associated with escalation
- Signal erosion: threat displays lose effectiveness as the frequency of bluff increases

# Cricket display costs

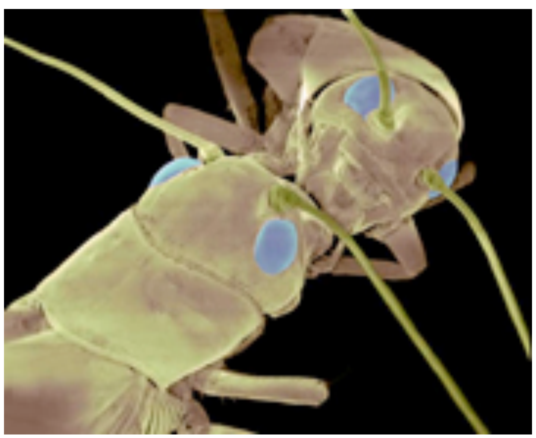


**Table 21.1** The agonistic display repertoire of the cricket *Acheta domesticus*

| Intensity level | Energetic cost | Context or function |
|---|---|---|
| Displays without contact | | |
| Cerci raise | 0.02* | Defensive act by loser or subordinate |
| Prebout stridulation | 0.02 | Owner signal |
| During stridulation | 0.02 | Mild aggressive threat |
| Postbout stridulation | 0.02 | Postfight victory signal by winner |
| Mandible flare | 0.08 | Aggressive threat, intention to bite |
| Shake | 0.49 | Postfight victory signal by winner |
| Tactics with light contact | | |
| Head butt | 0.37 | Ritualized fighting tactic |
| Foreleg punch | 0.37* | Ritualized fighting tactic |
| Mandible spar | 0.45 | Mutual ritualized fighting tactic |
| Antennae lash | 0.68 | Dominance maintenance |
| Stridulation lash | 0.70 | Dominance maintenance |
| Tactics with hard contact | | |
| Rear kick | 0.37 | Defensive act by loser or female guarder |
| Head charge | 0.61 | Overt attack, often by burrow intruder |
| Mandible lunge | 0.61 | Bite |
| Wrestling | 0.83 | Mutual mandible lock with head twisting |

# Little blue penguin fights

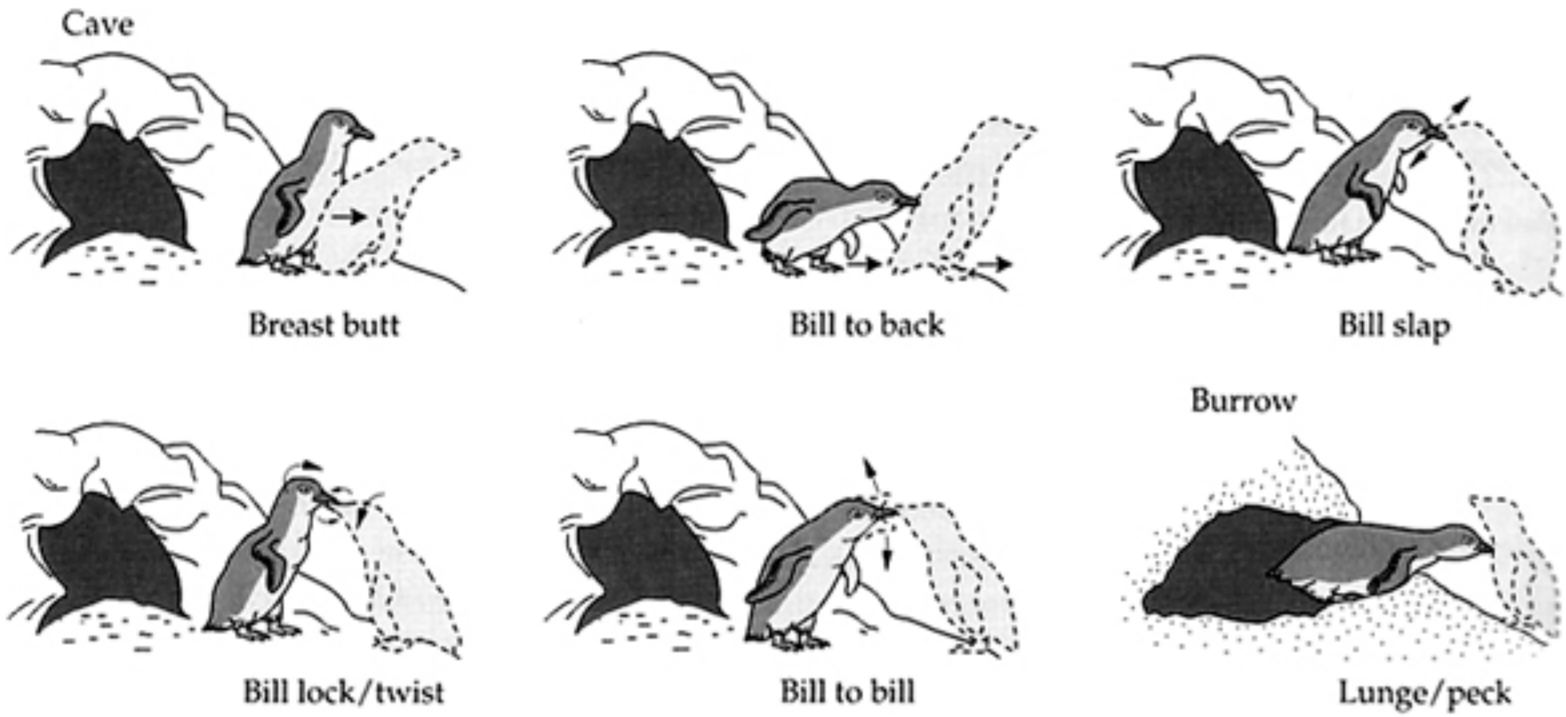



**Figure 21.14 Contact behaviors used by cave- and burrow-dwelling little blue penguins during conflicts.** Breeding pairs in cave-dwelling populations of the penguin (*Eudyptula minor*) nest colonially in large caves, whereas pairs in burrrow-dwelling populations nest in relatively isolated crevices. Cave-dwellers fight much more frequently than burrow-dwellers and possess five different contact signals shown here, compared to a single equivalent display (lunge/peck) in burrow-dwellers. Opponents are indicated with dashed outlines. (After Waas 1990b.)

Cave dwellers use more displays, but have fewer escalated fights

# Little blue penguin display repertoire

**Table 21.2** The agonistic display repertoire of cave-dwelling populations of little blue penguin *Eudyptula minor*

| Category | Risk level | Distance | Movement |
|---|---|---|---|
| Defensive, distance-increasing | | | |
| Low walk | 1 | < 1 | Away |
| Submissive hunch | 1 | < 1 | Away |
| Defensive, stationary | | | |
| Face away | 2 | < 1 | Stay |
| Indirect look | 2 | < 1 | Stay |
| Offensive, stationary | | | |
| Direct look | 3 | > 3 | Stay |
| Directed flipper spread | 3 | 2–3 | Stay |
| Point | 3 | 1–2 | Stay |
| Bowed flipper spread[a] | 3 | 1–3+ | Stay |
| Offensive, distance-reducing | | | |
| Zig-zag approach | 4 | 2 | Toward |
| Flipper spread approach | 4 | 1 | Toward |
| Contact | | | |
| Bill to back | 5 | 0 | Toward |
| Breast butt | 5 | 0 | Toward |
| Bill to bill | 5 | 0 | Toward |
| Bill slap | 5 | 0 | Toward |
| Bill lock/twist | 5 | 0 | Toward |
| Overt aggression | | | |
| Attack | 6 | 0 | — |
| Bite | 6 | 0 | — |
| Fight | 6 | 0 | — |

Penguins use many displays

Little difference in body size

# When should animals signal fighting ability vs motivation?

- If contestants only differ in fighting ability, then expect sequential assessment
  - Individuals often differ in body size or condition
- If contestants differ mainly in resource valuation, then contests should escalate and deescalate quickly
  - Signals and multiple display sets should reveal motivational level
  - Territorial systems, little body size variation
  - Previous experience likely affects contest outcome