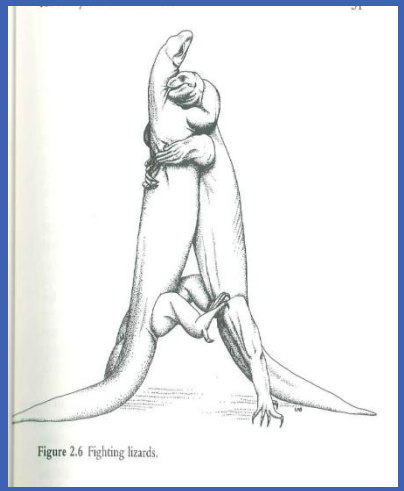
Figure 2.6 Fighting lizards.

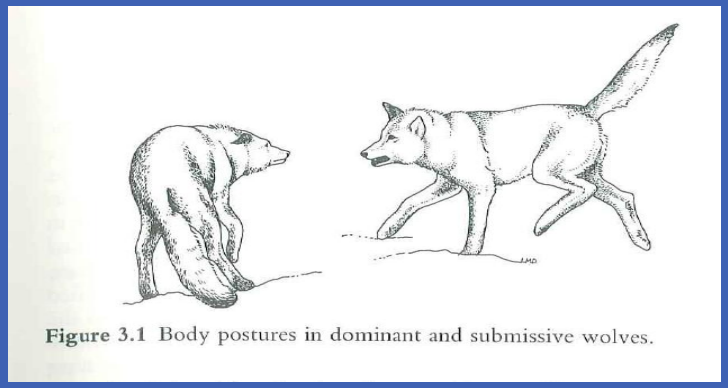
Figure 3.1 Body postures in dominant and submissive wolves.

Signals during social conflicts

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Ritualization

- Changes in function
- Changes in motivation
- Exaggeration of movements in size and frequency
- Freezing of movements
- More stereotyped movements
- Development of exaggerated physical structures

Main type of signals

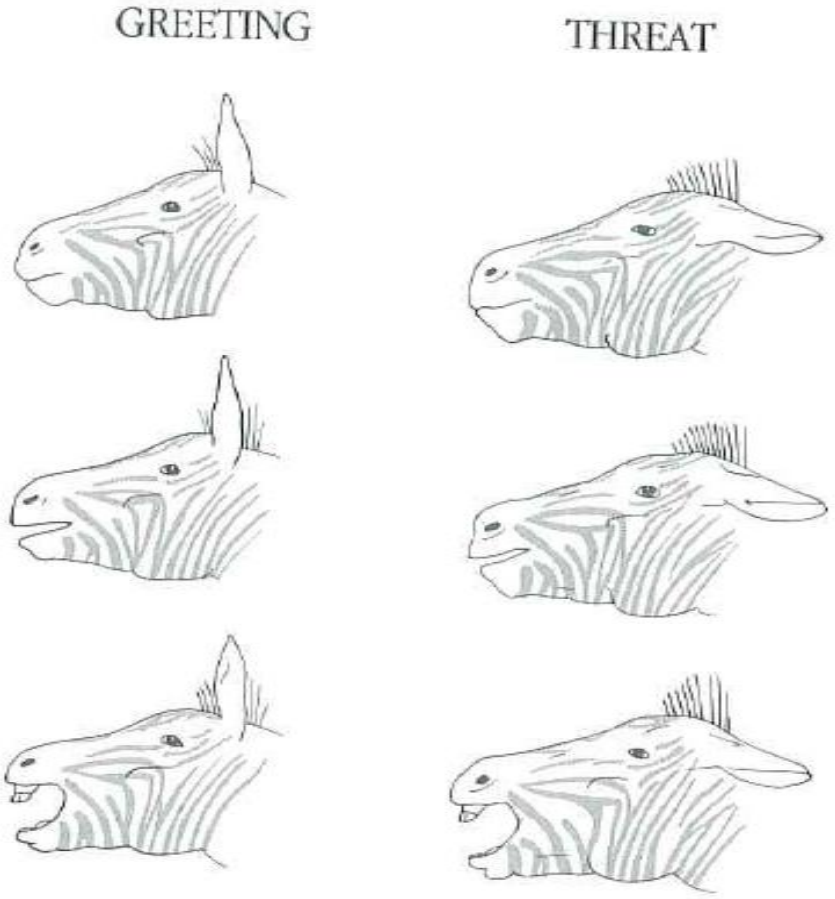
- **Graded signals:**
  - Vary in intensity and complexity
- **Discrete signals:**
  - On/off
- **Complex signals:**
  - Depending on the situation
  - More than one channel can be used

Combination of signals/channels

- Increases the amount of information to the reciever
- Increases the likelyhood that the receiver will get the message and understand it

- www.youtube.com/watch?v=pUgnghkeas4&feature=related

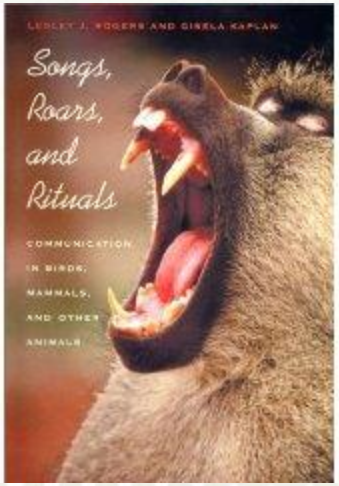
FIGURE 11-1 Composite facial signals in zebras
Ears convey a discrete signal. They are either laid back as a threat or pointed upward as a greeting. The mouth conveys a graded signal and opens variably to indicate the degree of hostility or friendliness.



Animal contests

- In any contest, competing individuals prefer different outcomes, yet signals may settle contests because the participants have common interest in avoiding an escalated fight

- Intension: A signaller may communicate information about what it will do next



Signals during social conflicts

- How can these signals be honest when the opponents wants the opposite outcome, namely that both want to win and that the other should lose?
  - The signal is an index, either of fighting ability (RHP) or of how important the resource is for the contestant. It is honest because the opposite is impossible
  - The signal is a handicap, that is: giving the wrong signal/cheating would be too costly for an individual with low competitive ability
  - Both of the contestant would benefit from avoiding an energy demanding and potentially harmful fight since there will be a cost both to the ultimate winner and the ultimate looser

Distinction between signals used in mate choice and contests

- A gross over-simplification: contests are often settled by indices, and mate choice by handicaps
- Signals during contest are usually indices of RHP, size, condition, or displays of weapons
  - Such signals can often be interpreted as ritualisations of cues used to predict intentions or fighting ability of an opponent
- In contrast, symbols (its form is unrelated to actual fighting ability), such as plumage, colour patterns and ornaments, long tales etc. are more common in mate choice

Symmetric and asymmetric conflicts

- Symmetric:
  - Equal chances
  - Waiting games: "War of attrition": contests are usually decided by persistence, and the winner is the contestant that hangs on the longest or that eats fastest
- Asymmetric
  - Contestants differ in one or more qualities

Asymmetries and asessment

- Three broad classes of asymmetries thay can bias the outcome of a dispute (Maynard Smith and Parker, 1976):
  - RHP (resource holding potential)
  - Payoff asymmetries
  - Uncorrelated asymmetries

RHP

- Resource holding potential=competitive ability=fighting ability

- Individuals are likely to differ in their fighting- or competitive ability (Barnard, 2004):

  - If two individuals differ in RHP, the weaker one should witdraw as soon as it assesses its chances of winning as low

  - Persisting beyond this point, or escalating (becoming more agressive) before a decision has been reached, wastes time and risks injury to no good effect

Indices of RHP

- Vocal sound/pitch (i.e. the roar of the red deer stag)
- Horn (size) or display of other weapons
- Strong colours and colour patterns
- Actual body size
- Condition and vigour
- Other examples:
  - Depth of the croak in Common Toads
  - Tigers scratching a tree as high as they can reach to mark their territory
  - Funnel-web spiders vibrating a web
  - Shrimps spread their claws

Displays of weapons

- Wolves display their canines
- Stag beetles display their ”antlers”
- Crabs display their claws
- Horns in Bighorn sheep, wild mountain goats and many other ungulates

• Ram groups – social structure

- **Dominance:**

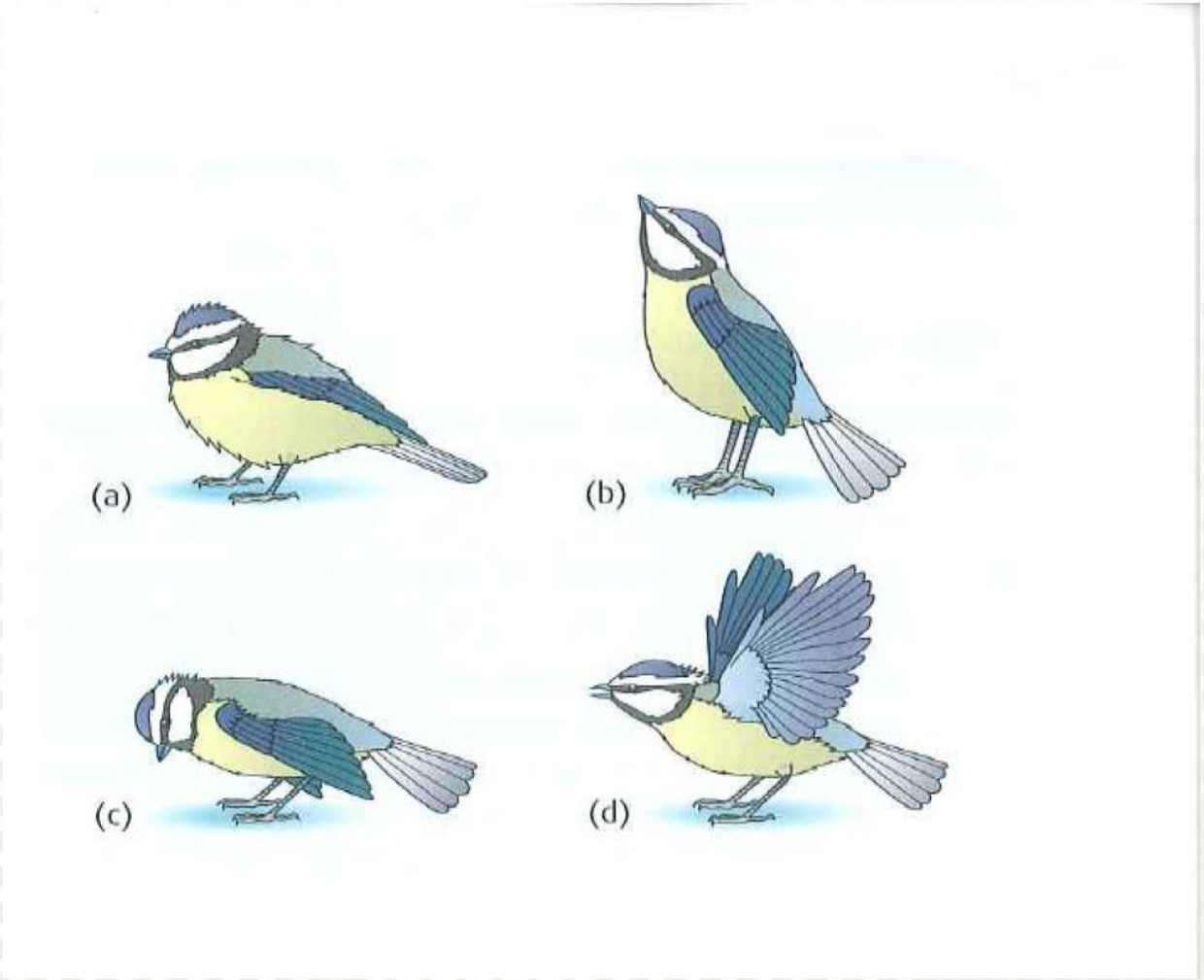
1. Size of horns
2. Size of body

Social status

- Sosial status horses:

- http://www.youtube.com/watch?v=7DCmd1N4D-0

Postures during agonistic encounters in blue tits



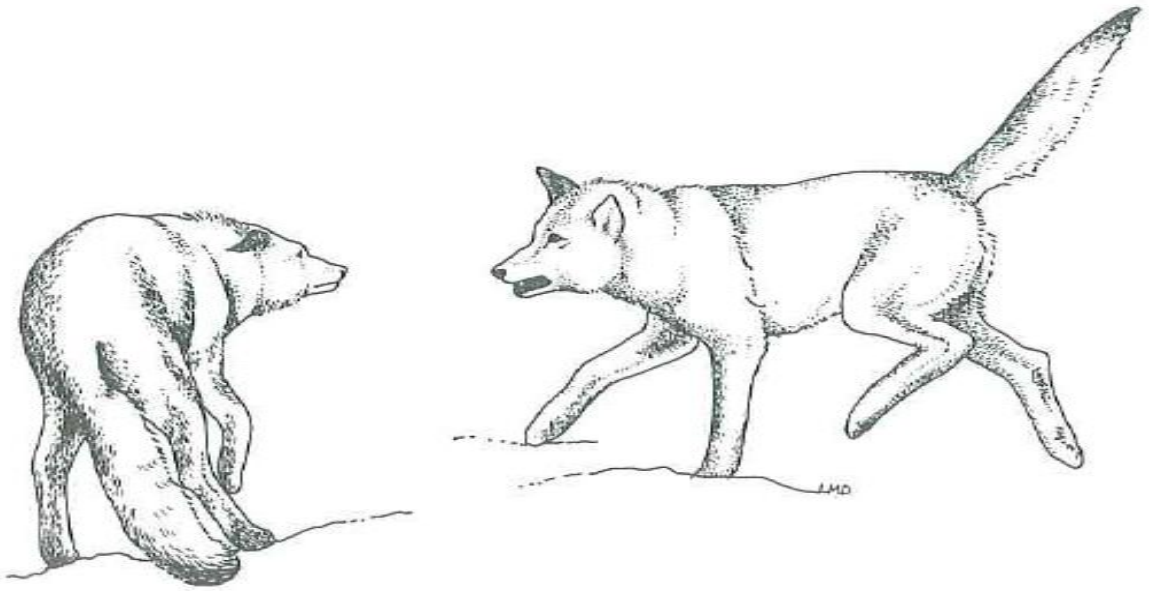


Figure 3.1 Body postures in dominant and submissive wolves.

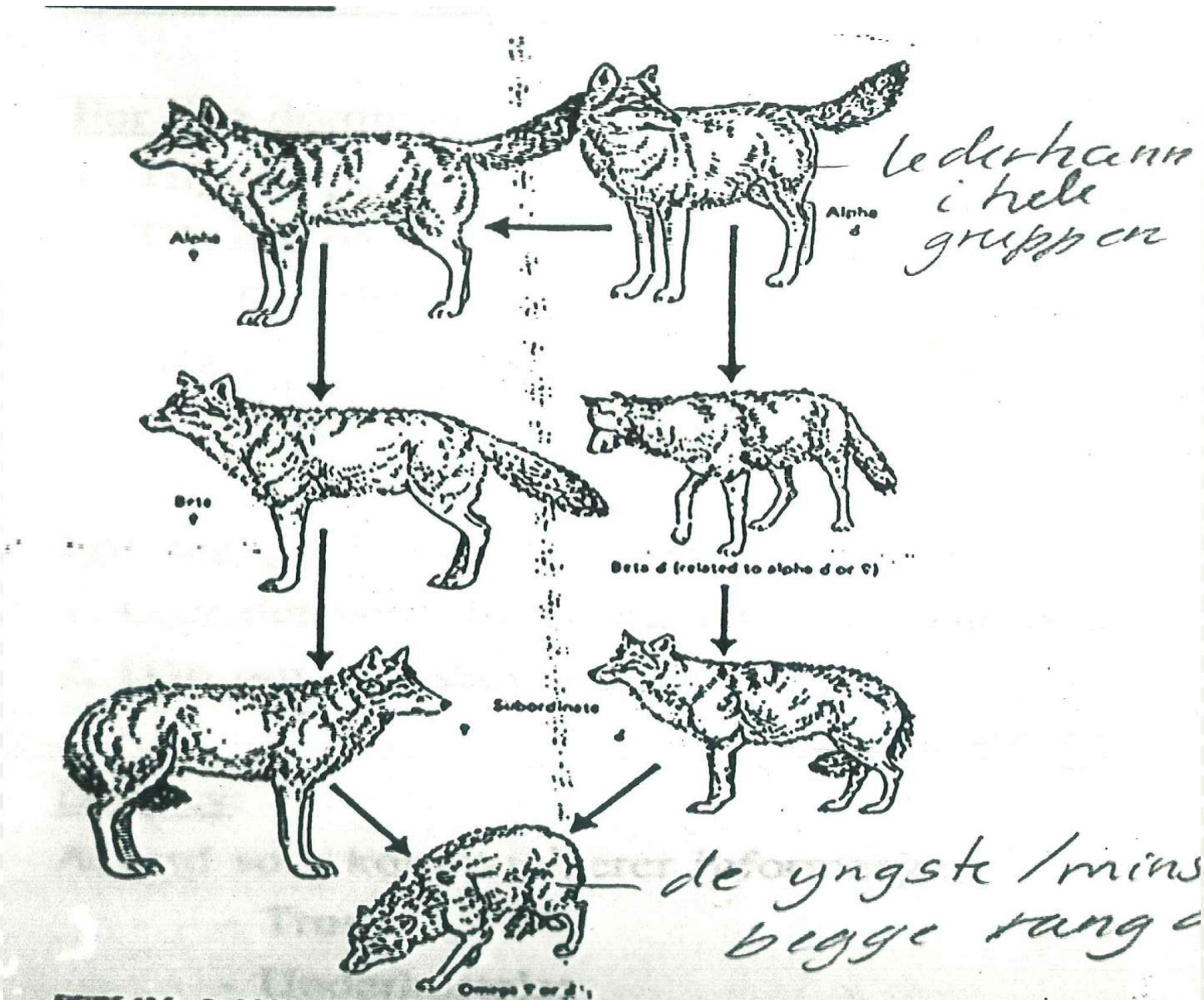
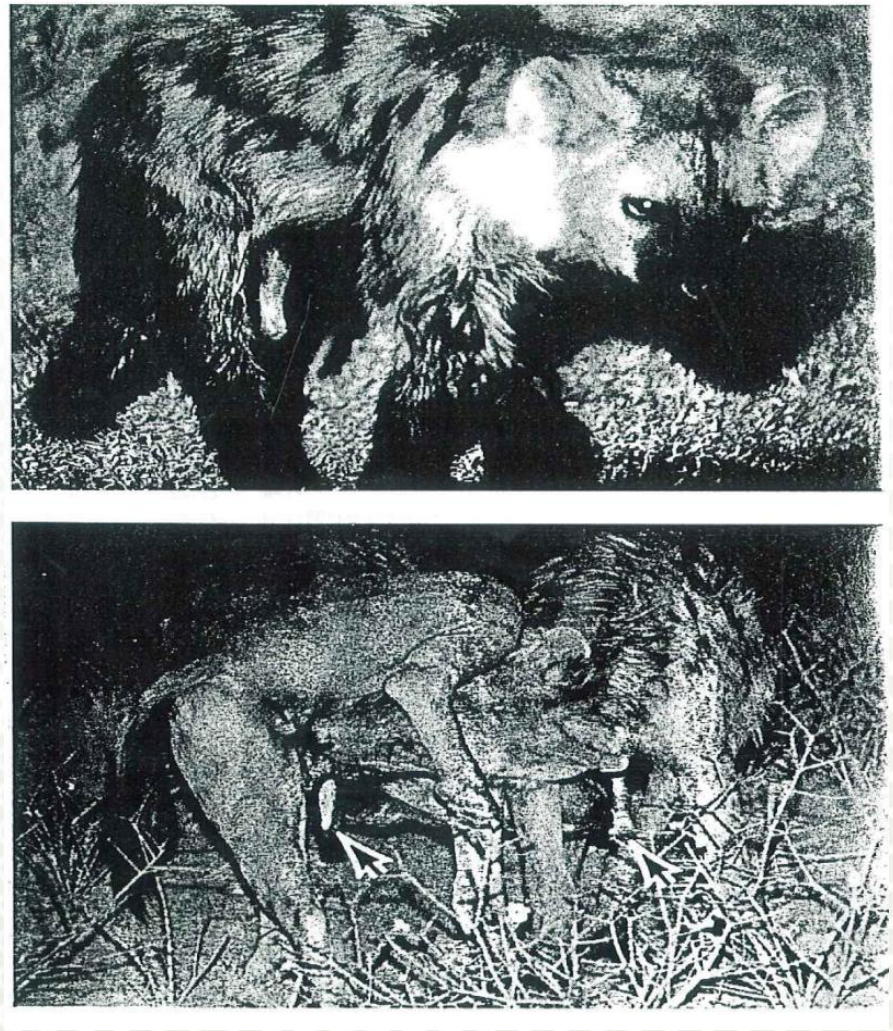


FIGURE 13.6 Social hierarchy in a small wolf pack. Note the two separate hierarchies, one male and one female, with one individual occupying the omega position. The alpha male is the dominant individual in the pack.

(Smith, 1992)

- www.youtube.com/watch?v=5Pnthmz0IMQ

The pseudopenis of spotted hyena females – an adaptive signal of status?



Plumage (Colour patterns/stripes) as a "status badge "

- Examples from birds:

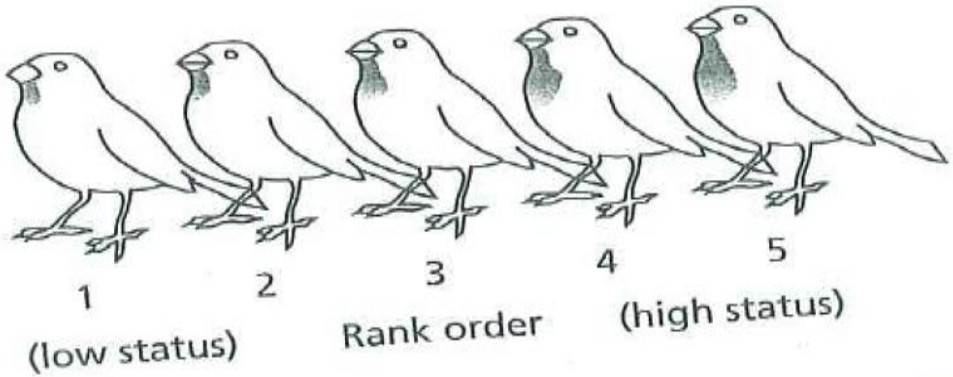


Figure 11.8 Social status in male house sparrows is reflected in the size of their black bib. See text. After Møller (1987c).

Plumage (Colour patterns/stripes) as a "status badge "

- If the difference between dominant and subordinate birds appear to be just a matter of a bit of pigment in feathers, why do not subordinates simply develop bibs and cheat?? There is no obvious physiological constraint

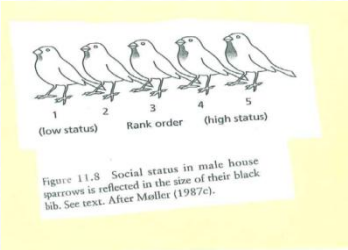


Figure 11.8 Social status in male house sparrows is reflected in the size of their black bib. See text. After Møller (1987c).

  - Social policing: Declaration of high status has to be supported by appropriate behaviour
  - But: does not explain why they cannot add both colour and testosterone levels?
  - The answer to this might thus be that increased hormone activity and energy spent on fighting use up resources that subordinates could not afford or that other testosteron effects such as immune depression would be too detrimental
  - Bib size is not only correlated to testosteron but also to metabolic rate and antibody production: bib status badge is a honest reflection of underlying male quality
  - So status badges might be cheap to produce but costly to maintain

Pay-off asymmetry (Barnard, 2004)

- Even when the contestants are evenly matched in RHP, one of the opponents can be preparesdto persist for longer and escalate further because it has more to gain from winning
  - A disputed food item is more valuable for a hungry animal
  - A disputed shelter is more valuable for an animal suffering form severe heat loss or fear
  - The resident and intruder might estimate the value of the territory differently

Uncorrelated asymmetries

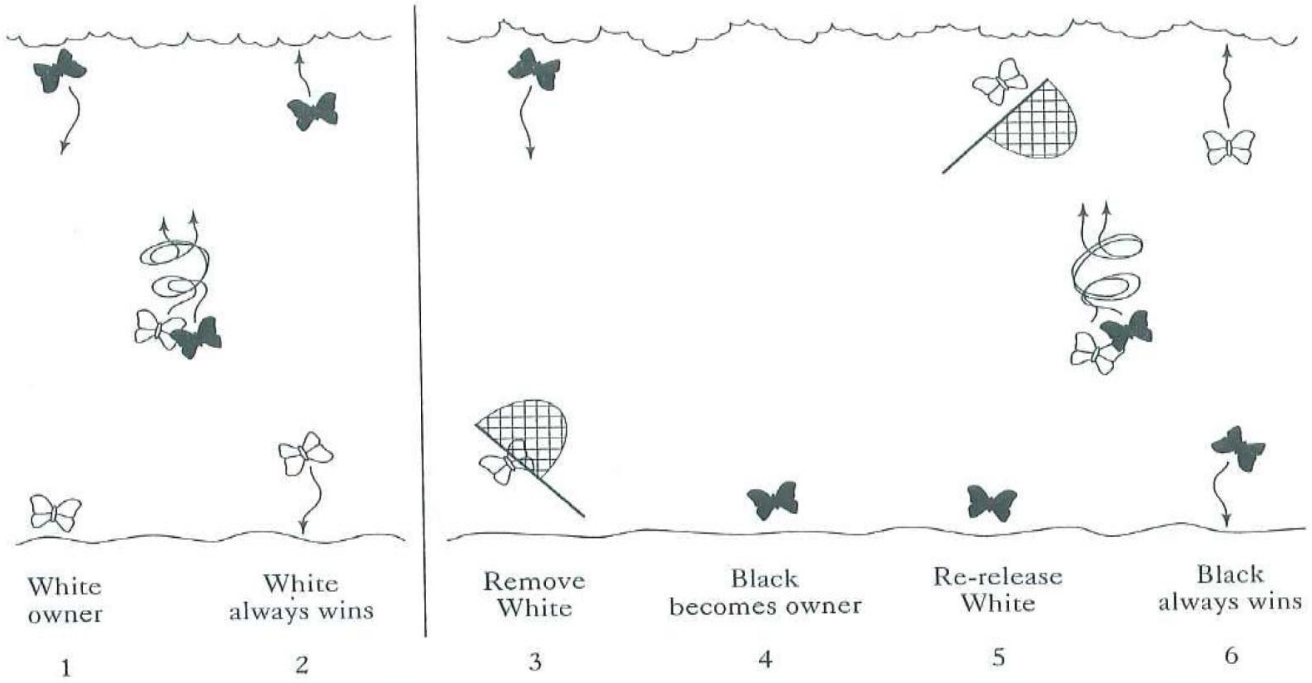
- Contestant need not to differ in either RHP or expected payoff to be settled
  - Contests could be decided on the basis of some purely arbitrary convention:

    Ownership (uncorrelated to RHP and payoff)

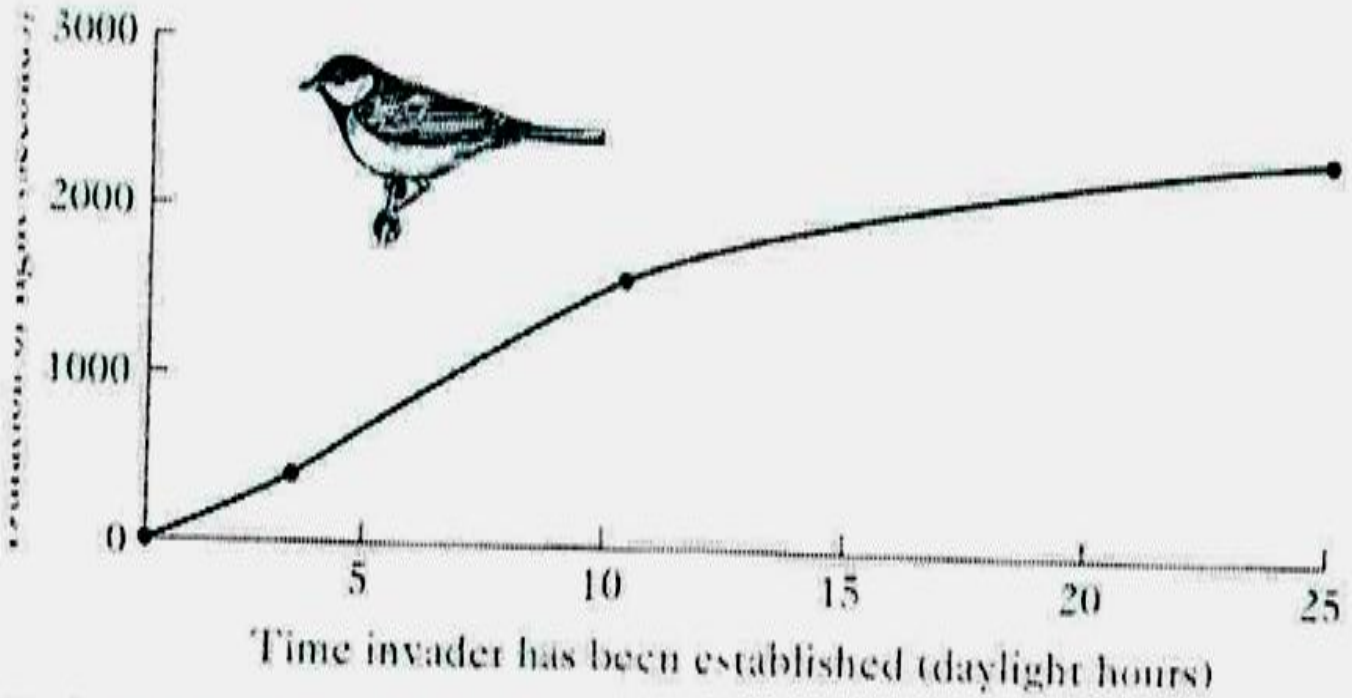
Indices of ownership

- Examples: scent-marking by mammals (Gosling, 1982), calls (Wagtails; davies, 1981) or other vocalisations
- If owner play Hawk, if intruder play Dove:
  - Maynard Smith and Price` (1973) game theoretical model assumed that all contests were between owner and intruder. If this was true, indices of ownership would be irrelevant because the intruder always knows that the opponent is an owner
  - This assumption often do not hold, for instance if the contested resource is a new territory, both opponents are sometimes intruders

Ownership – a butterfly example



32 **The resident always wins?** An experimental test of the hypothesis that territorial resident males of the speckled wood butterfly always win conflicts with intruders. When one male ("White") is the resident, he always defeats intruders (1,2). But when the resident is temporarily removed (3), permitting a new male ("Black") to settle on his sunspot territory (4), then "Black" will defeat "White" upon his return after release from captivity (5,6). *Source: Davies [266].*



6 **A test of the payoff asymmetry hypothesis.** In great tits, the more time a new resident has been on a territory, the longer the fights between that individual and the original resident (which was temporarily removed from his territory by the experimenter). *Source: Krebs [675].*

Conceptual ESS Models Applied to Animal Contests (Maynard Smith and Price, Parker, Enquist and Leimar and their groups……)

- What is an evolutionary game?
  - A model in economic decision theory describing the potential interactions of two or more individuals whose interest do not entirely coincide
- What is an ESS?
  - A strategy with the following property: If all members of a population are genetically coded to play this strategy, any initially rare mutant strategy would receive negative selection pressures in this population
  - A strategy which when adopted by most members of the population cannot be beaten by any other mutant strategy
- A Nash Equilibrium:
  - Is a combination of strategies for the players of a game, such that each player`s strategy is a best response to the other players` strategies
  - A best response is a strategy which maximizes a players` expected payoff against a fixed combination of strategies played by others

"The War of Attrition Model"

- The one that continuous longest wins the disputed resource!

- Contest length:

Empirical support:

- The length of the time that male dungflies wait for visiting females in one cowpat to mate with (but do not fit when looking at the length of time when two males struggle for one female)

The ”Hawk-Dove” Game

- The opponents do not differ in any qualities, so the game is per def. symmetric
- ”Hawks” escalate until injured or until opponents retreat
- ”Dove” diplay, but retreat if opponent escalates

- If all individuals in a population were doves, then a mutant Hawk would be very successful and start spreading– so no ESS, and if all were Hawks, a mutant Dove would do better in terms of payoff (based on predefined values H vs H=-25, Dvs H=0, H vs D=+50)
- A mixture of Hawks and Doves might be stable
- An ESS would be when the average payoff for Hawks are equal to the average payoff for Doves

The "Sequential Assessment Game" (Enquist, Leimar etc.)

- Many species show a repertoir of behavioural patterns used in in constest over resources
- It is likely that the fuction of these behaviours is the asessment of asymmetries between contestants in physical variables
- The War of Attrition Model and the Hawk Dove Game do not incorporate any behavioural mechanisms allowing assessment
- In an SA-game, assessment of asymmetries is a major activity during a fight
- Empirically tested on Cichlid fish, butterflies, spiders, sea gulls and pigs

Assumptions and predictions from the SA-model

- A1:The behavioural diversity often found in fighting behaviourreflect different methods for asessing asymmetries between contestants
- A2: When relative fighting ability is assessed through sampling of correlated asymmetry, there will be a diminishing return of information with each repetition of the behavioural element
- P1: An individuals probability of winning should increase when its fighting ability increases relative to its opponent
- P2: The behavioural sequence should be organised into phases
- P3: The behavioural sequence should be independent of relative fighting ability
- P4: Decisions to give up should be influences by fighting ability: contests with a smaller asymmetry in fighting ability should proceed further along the behavioural sequence
- P5: The total cost of fighting should increase when the asymmetry in fighting ability decreases

Empirical tests on Cichlid fish showed that fights were devided into phases:

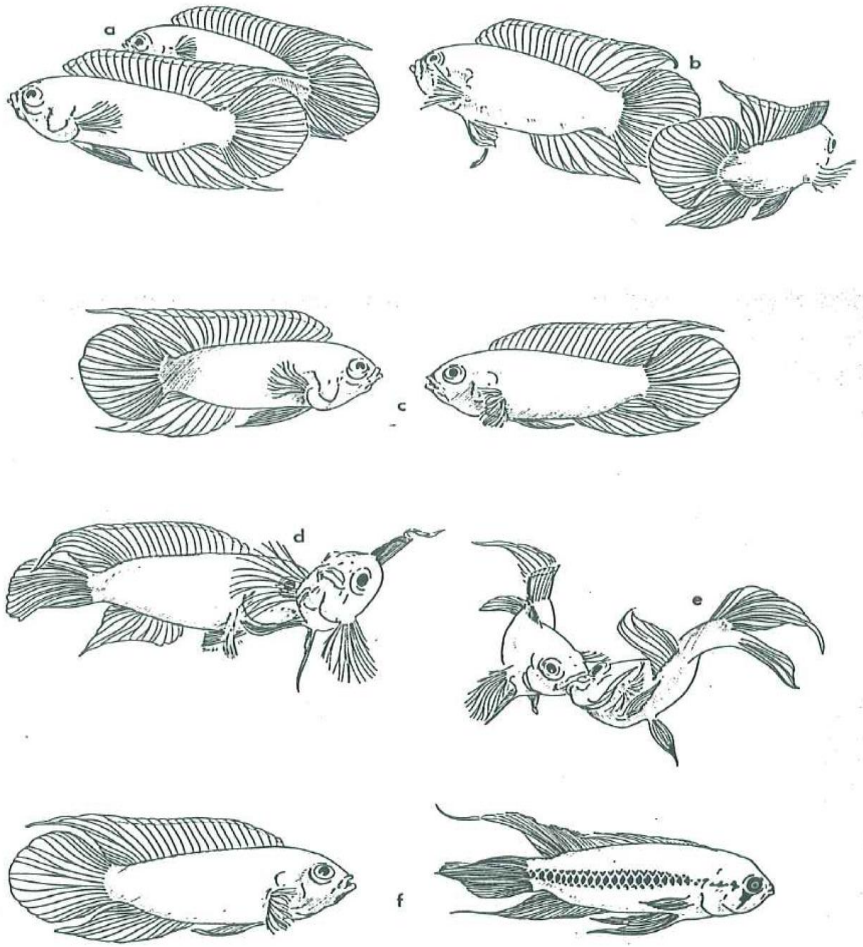


Fig. 7.7 Fighting sequence of male cichlid fish, *Nannacara anomala*. (a) Lateral orientation. (b) Tail-beating. (c) Frontal orientation. (d) Biting. (e) Mouth wrestling. (f) The loser (right) gives up. Drawing by Bibbi Mayrhofer. From Jakobsson *et al.* (1979).

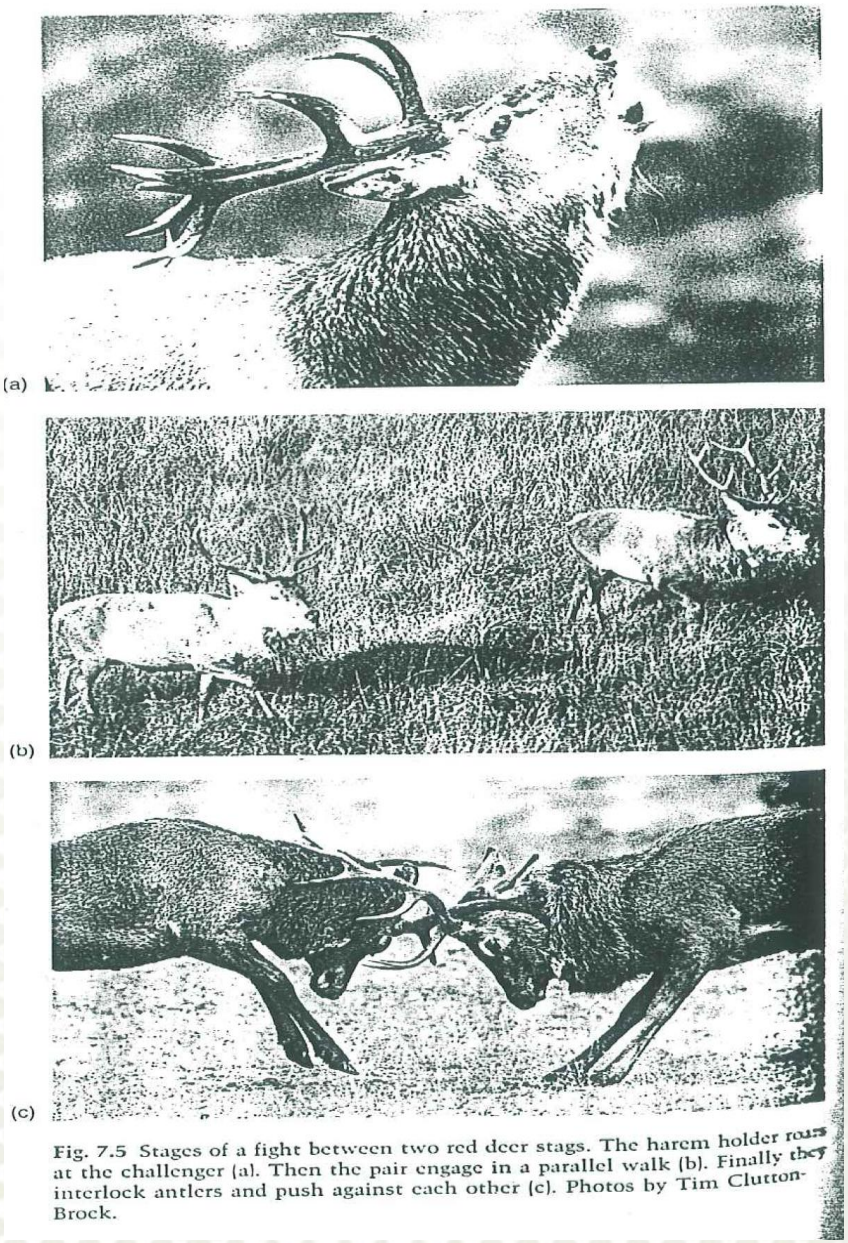
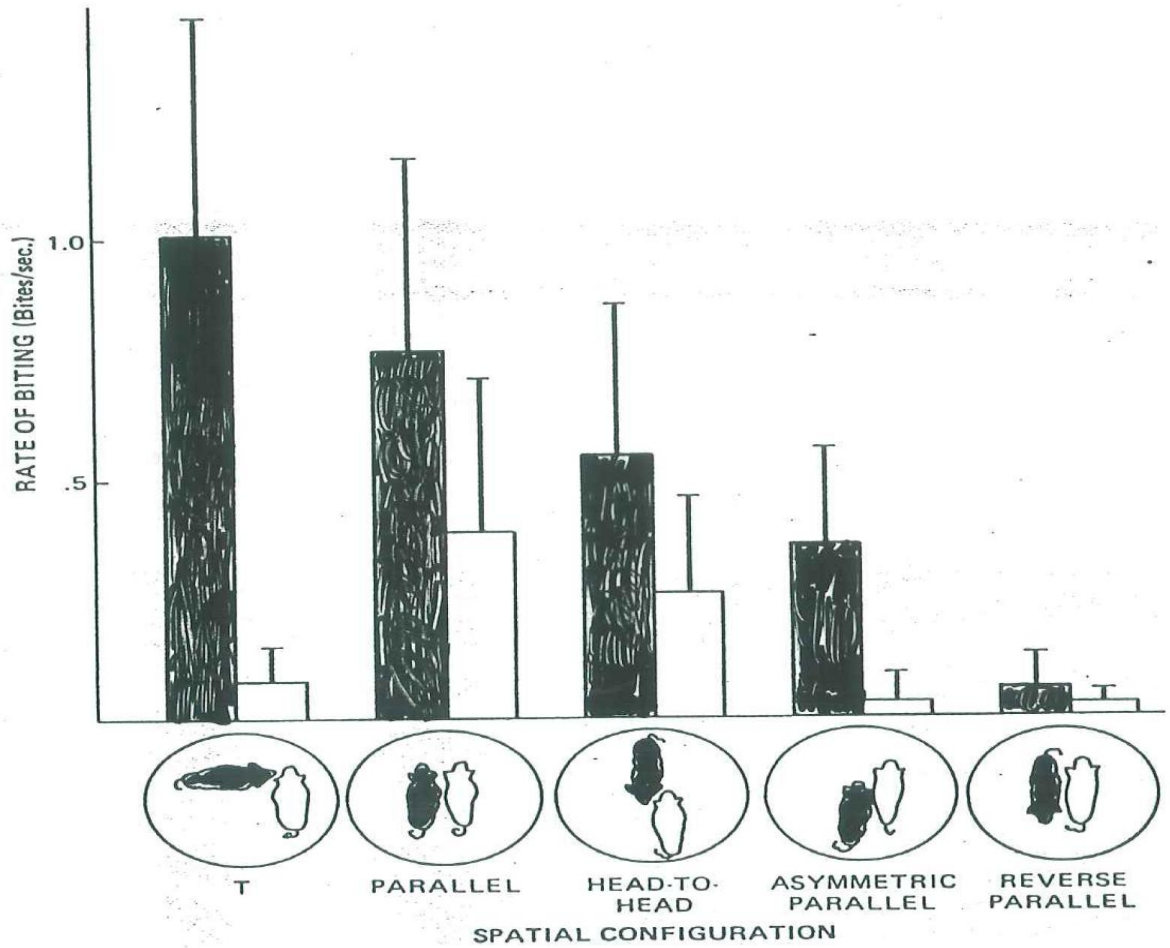
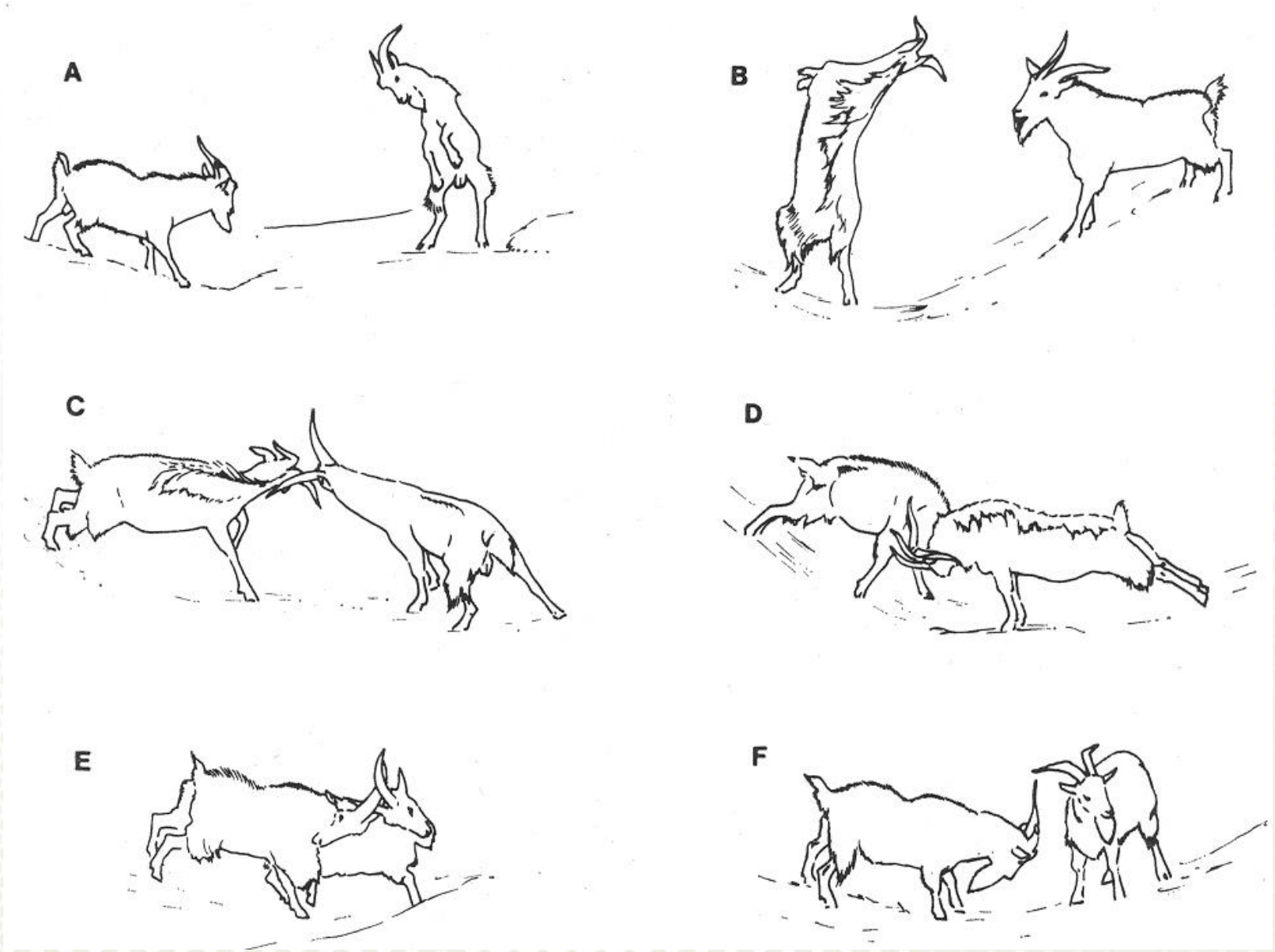


Fig. 7.5 Stages of a fight between two red deer stags. The harem holder roars at the challenger (a). Then the pair engage in a parallel walk (b). Finally they interlock antlers and push against each other (c). Photos by Tim Clutton-Brock.



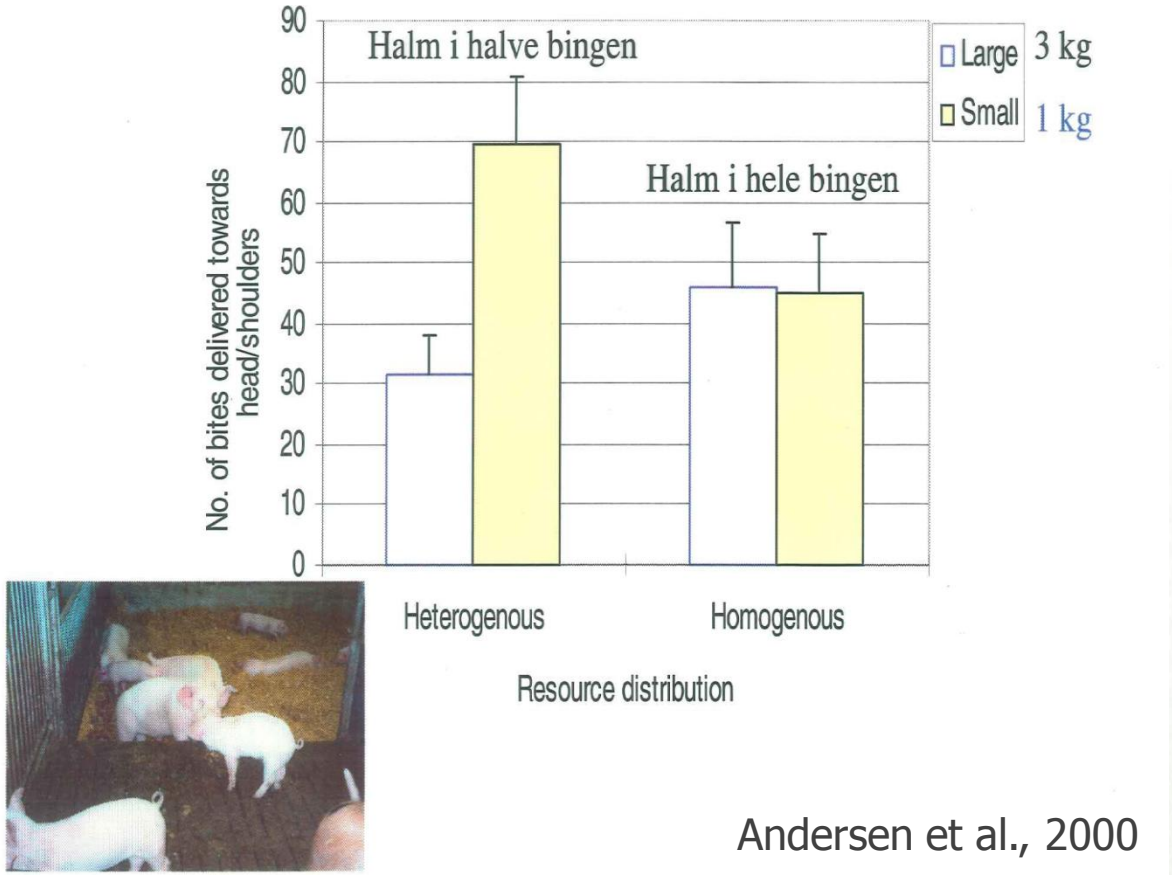
g. 1. Mean (+ SD) rate of biting in each spatial configurations by the pig of each pair that bit equently (shaded) and the pig that bit less frequently (unshaded) while in that configuration.

(Rushen, 1989)


A
B
C
D
E
F

The SA-model applied to pigs (Andersen et al., 2000)

- Predictions made:
  - The number of bites delivered and fighting duration should be negatively correlated to weight asymmetry
  - The total costs of fighting should increase when weight asymmetry decreased
  - The probability of winning should be highest for the largest pig
- Weight differences were 1 vs. 3 kg + resource in half the pen vs. resource in the entire pen



Andersen et al., 2000

Fighting duration was significantly shorter in groups with large weight asymmetry

Irrespective of resource distribution.

The number of bites delivered was lower in groups with a large weight asymmetry,

but only when the resource was limited to half the pen.

The comination of small weight asymmetry and a limited straw area resulted in the greatest number of bites.

The largest pig won around 50% of the fights, and 25% of the variation in percentage offights won was explained by weight asymmetry.

Communication during collaboration

www.youtube.com/watch?v=E4fIiijYiOY

Game theory and cooperation (Dugatkin and Reeve, 1998)

- There are at least three ways that cooperation can evolve among unrelated individuals:
  - Reciprocity
  - Group selection
  - By-product mutualism

Reciprocity

- ”Tit for Tat”: A strategy that instructs players to cooperate when first meeting an opponent, and to subsequently copy whatever that opponent does. This has four main key features:
  - 1. It is nice (always starts with cooperation)
  - 2. It is retaliatory (defects in response to defection)
  - 3. It is forgiving (but it only remebers one step backward)
  - 4. Success or failiure of cooperation will depend on the probability of future play with the same player

”By-product Mutualism”

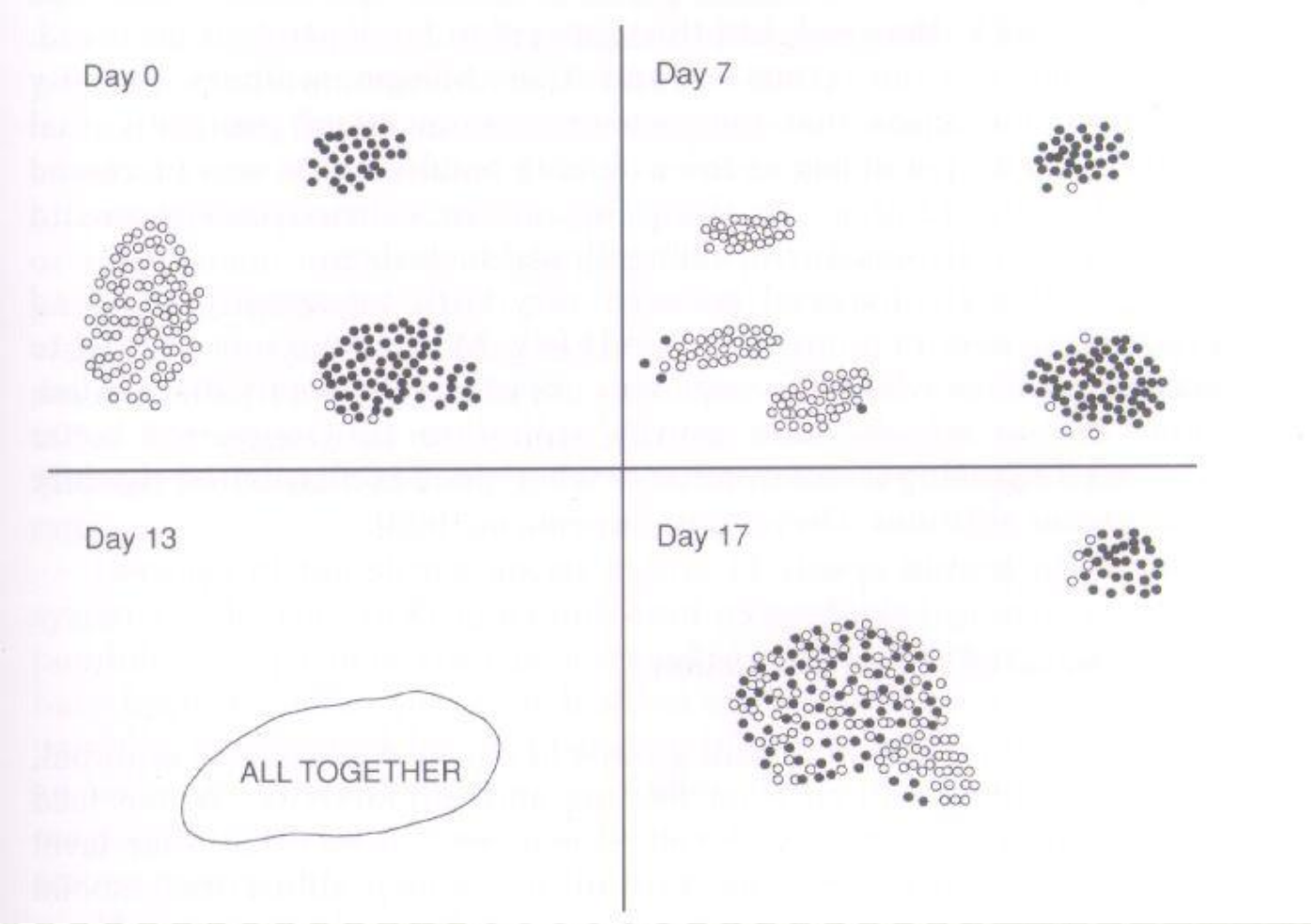
- Each animal must perform a necessary minimum itself that may benefit another individual as a by-product
- These are typically behaviours that a solitary individual must do regardless of the presence of others, such as hunting for food. These activities are more profitable in groups
- Another example is territorial defense where it might also be situations where it is beneficial to get help from others, such as in pied wagtails defending river banks

Group selection (as opposed to R. Dawkins (1976): ”The selfish gene”)

- Cooperation can evolve even when it has a cost to the individual performing it, if within-group cost is offset by some between-group benefits, such that cooperative groups are more productive than selfish groups
- For such group-level benefits to be maifested, groups must differ in the frequency of cooperators within them, and groups must be able to export productivity associated with cooperation
- Examples : raiding and warfare in chimpanzees

Merging groups

- McBride et al., 1967



Channels for social communication in domestic species

Poultry

- Visual signals through postures and vocalisations
- Vocalisations during territory defense
- Coloured feathers, quality of feathers and the size of the comb are important indices of social status

Cattle

- Visual signals (body postures) are most important
- Some vocal communication, but not as pronounced and varied as for instance in pigs
- Olfactory communication is important, especially during courtship and mating

Pigs

- Olfaction/smell important for status signalling in boars
- Olfaction is extremely important in social groups
- Large variety of sounds used in social groups
- Visual signals less important
- Tale- and ear position

Sheep

- Olfactory, visual and vocal (many frequencies) all used
- Courtship and aggression mainly through visual signals

Horses

- Visual signals most important
- Facial expressions, ear- and body postures more detailed than in cattle and pigs
- Olfaction is important for social recognition


The End