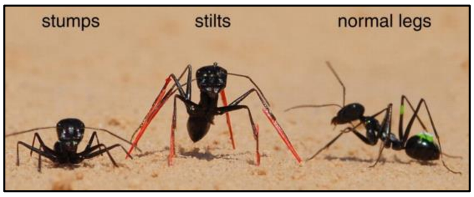
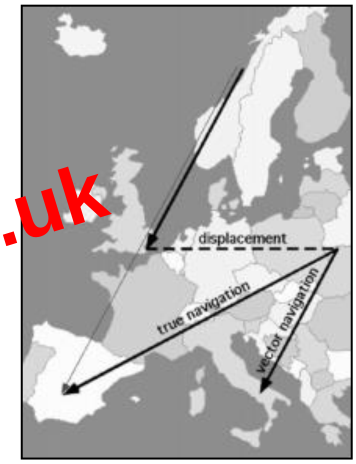
- E.g. The desert ant (contradictory findings below??)



  - Easy to manipulate → Used extensively in research
  - Demonstrated to use a more efficient homebound route (113m) than outward foraging route (345m)
  - Also demonstrated to use 'odometer' in navigation – Foraging ants were collected and manipulated (stumps/stilts) then allowed to return to nest
  - Stilted ants overshot the nest, stump ants undershot the nest (then initiated random search) and control ants found the nest
  - The ants were then allowed to complete a whole foraging journey – All of which completed it correctly – Leg length was irrelevant – Ants were using an internal odometer to count outward journey steps, then repeat that on the homebound journey
- **Limitations**
  - **Odometer is error-prone** – Potentially severely disrupted by displacement → Inaccurate (e.g. if an individual is blown by wind or falls off a rock)
  - **If disrupted** → Initiates random or systematic search → **May result very far from intended target**
  - **Limited to navigating to a known home/nest site** – Unsuitable to locate novel habitat patches

Animal navigation 2 – Complex navigation strategies between true navigation

<u>'True' navigation</u>

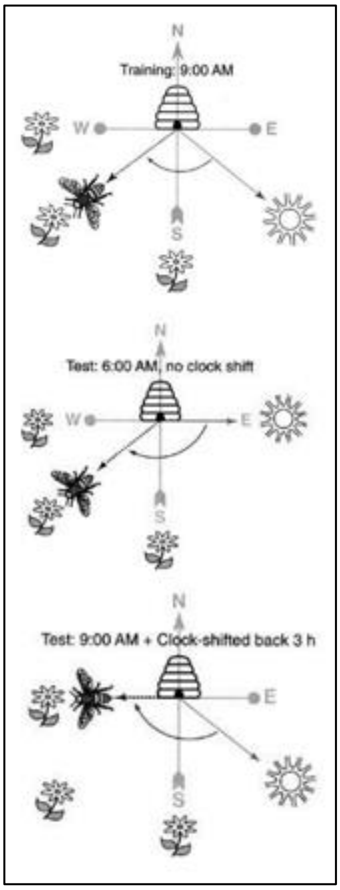


- **True navigation** = Navigation to a point outside of an individual's sensory range (e.g. Manx shearwaters long distance overwintering)
- Well-studied discipline of animal behaviour – Tested in many animals (especially birds)
- Involve displacement experiments both in field + laboratory experiments
  - Movement to an unfamiliar area (outside of sensory range) to determine an ability to determine location and navigate in the right direction from there
  - E.g. Displacing a migrating bird to test whether it (1) Adjusts its trajectory to reach the intended location or (2) continues along their vector navigation at the same bearings as before displacement

<u>Requirements for true navigation</u>

- Could be the result of several different mechanisms combined
  1. **Internal map** (location) – Knowledge of geographical position
  - Magnetic, olfactory, cognitive (lecture 3)
  2. **Internal compass** (direction – simpler concept) – Knowledge of the bearing (i.e. direction of travel) of a goal
  - Sun, star, magnetic
- (1) + (2) are often translated using global sensory systems

<u>'Time-compensated' sun compass</u>



- Position of the sun in the sky at certain times of day provides indication of direction
- Used by many day-navigating animals (e.g. bees)
  - Individuals learn (1) when to forage (2) which specific plants to forage by calculating the angle between the sun and intended (reward) foraging site, based on time of day
- Practical example – Do bees use a sun compass to navigate?
  - Tested using clock-shift experiments under artificial laboratory conditions (i.e. controlled light exposure to stimulate different times of day)
  - Bees trained to forage at 9am
  - At 6am (not clock-shifted) – Bees successfully reach intended foraging site, despite angle being different (by using sun compass correctly)
  - Clock-shifted 3hr back – Bees 'think' it is 6am (under artificial light) when it is in fact 9am (under natural light), resulting in utilising the 6am angle and navigating to an unrewarded flower (by using sun compass correctly)

- The minimum exposure time (24hr) required to initiate increased mating duration is important in the natural environment to ensure increased (costly) effort is only commenced if threat of competition is sustained – Rules out short term ‘unthreatening’ exposure of every male an individual comes in contact with

<u>Behavioural plasticity in combination with strategic ejaculation</u>

- Behavioural changes (e.g. increased mating duration) have fitness consequences in combination with an ejaculate response
- **Does production/transfer of seminal protein (e.g. sex peptide) alter in response to cues to competition in *D. melanogaster*?**
  - Results – Indicate males exposed to competition do transfer more sex peptide
- **How does sperm production/transfer differ under competition in *D. pseudoobscura*?**
  - Produces 2 types of sperm
  - (1) Long fertilising sperm (2) Short non-fertilising sperm – Suspected ‘cheap filler’ or acts to protect (1)
  - Results – Males kept with a rival were found to produce/transfer more (1)
  - Findings consistent with *D. melanogaster* – Only able to produce one type of sperm (fertilising)
- **Conclusions – An ejaculate response often accompanies a behavioural response (e.g. increased mating duration)**
  - Both responses are costly to the male and should only be invested in if long term competition is anticipated

<u>Is there evidence in a trade-off in resources when responding to competition?</u>

- Males must invest limited resources wisely into various factors enhancing reproductive fitness (e.g. ACP production)
  - A plastic response should therefore theoretically have (1) associated benefits AND (2) associated costs
- Experiments have also studied the associated costs of reproduction on males
  1. **Mating males in rapid succession to multiple females**
  - Results – Exhausted production of ACPs → Accessory gland depletion → Fewer offspring produced
  2. **Mating success compared between males (1) isolated for entire lifespan (2) exposed to a rival for entire lifespan**
  - Results – (1) Invested less effort into each mating → Lived/reproduced longer
    – (2) Invested more effort into each mating → Aged faster + died younger
    – Similar overall offspring production – Demonstrates trade-off in resources

<u>How do males assess competition?</u>

- Varies between species – Extensive evidence of:
  - Smell (cuticular hydrocarbons) – E.g. Voles, newts, mealworms, beetles
  - Song – E.g. Field crickets
- Combination of cues – E.g. *D. melanogaster*

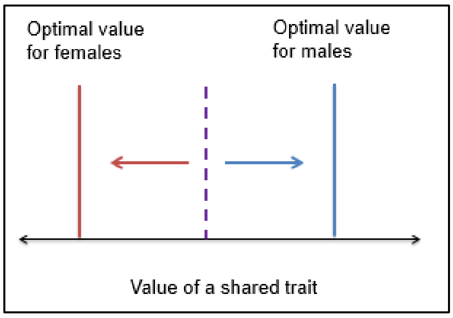
<u>Use of cues in *D. melanogaster*</u>

- Studies have been conducted on the impact of sensory input on observed fitness output/behavioural change
- Involve combination of (1) genetic (2) physical manipulation to remove male’s ability to detect sensory cues from other males
  - **Removal of song** → (1) Preventing rival producing song by removing wings (2) Using mutants that couldn’t hear
  - **Removal of smell** → (1) Stimulate presence of a rival using cuticular hydrocarbons (2) Use of mutant lacking smell-detection odorant binding protein (3) Removal of 3rd antennal segment
  - **Removal of vision** → (1) Kept in darkness (2) Using mutants with vision defects
  - **Removal of touch** → (1) Separating males by nets
- Individual/independent removal of cues → Males still able to respond – Suggests uses of multiple cues
- **To determine importance of each dependent cue, cues were taken away in pairs**
  - I.e. Exposure to smell and hearing but not touch and vision, etc
- **Results**
  - Control (unmanipulated) males exposed to all cues AND any paired manipulation involving vision → Males still able to respond – Suggests vision is unimportant
  - All other combinations → Males unable to respond significantly to presence of a rival male – Suggests males use complex interactive touch, smell, and hearing cues to assess competition in their environment

Sexual selection 3 – Sexual conflict: The real battle of the sexes

Introduction to sexual conflict

- Research started in the mid-1990s and is gathering pace
  - Parker developed the concept of sexual selection being a consequence of polyandry
  - Promiscuity → Sperm competition → Selection to best increase an individual's own reproductive output → Conflict
- **Sexual conflict =** Conflict (i.e. decoupling) between the evolutionary interests of individuals of the two sexes
  - Any deviation from monogamy → Interests between sexes become increasingly unlinked
- Despite sharing most of the same genome, slight differences between Ms + Fs → Differing priorities/interested
  - Traits that make a good F don't necessarily make a good M
  - Conflict exists over the 'value' of a particular unshared trait between the sexes
  - The optimum value for a F might differ from that of a M → Tug of war over trait's value → Ms + Fs attempting to evolve the trait differently
  - This value might stabilise at a mid-point between the two differing optimums



- 2 forms – Both have effects on evolution
  1. **Intralocus conflict** (might drive sex-biased expression and constrain evolution)
  - The same gene (or set of genes) is controlling a trait expressed in **both sexes**
  - E.g. (1) Zebra finch bill colour and (2) human height
  2. **Interlocus conflict** (might drive co-evolutionary arms races and speed up evolution)
  - The trait is only expressed in **one sex**, but influences a **shared trait**
  - E.g. (1) Sexual cannibalism in garden mantis (2) Seminal proteins in *D. melanogaster* and (3) Antennal graspers in water striders

Interlocus conflicts

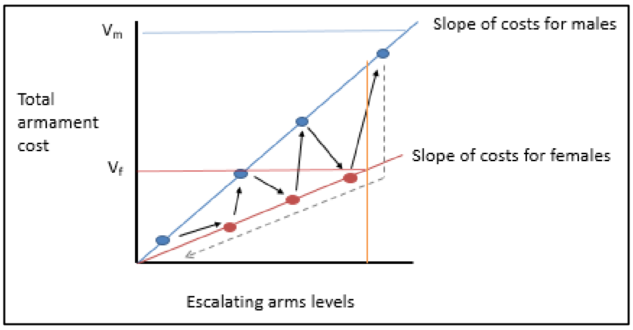
- **To demonstrate this conflict is happening we must:**
  1. Find a trait genetically determined (i.e. heritable) and positively genetically correlated to both sexes (i.e. same gene/set of genes underlying the trait for both sexes)
  2. Demonstrate that Ms and Fs have different optimal values for the trait (i.e. correlation between trait and fitness is opposite in either sex)

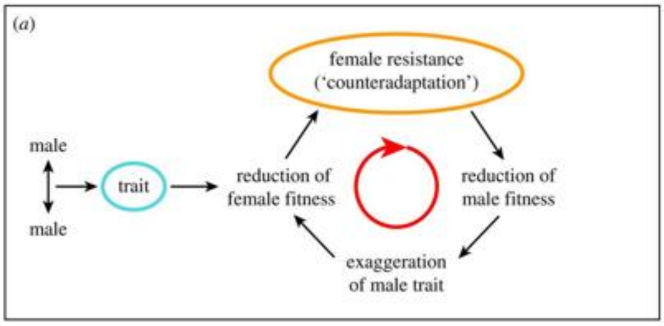
- **E.g. Zebra finch bill colour**
  - Males generally have much redder bills → A sexually selected (and costly) trait
  - Criteria was met
    1. Heritable + positively genetically correlated – Within-family bill colour was more similar than unrelated individuals
    2. Negatively phenotypically correlated – Intensity of bill colour determines offspring output (unresolved conflict)
       - For males, darker bill → Increased offspring output
       - BUT for females, darker bill → reduced offspring output (costly but not beneficial)
- **E.g. Human height**
  - Males are generally taller than females → A (somewhat) sexually selected trait
  - The reproductive output for relatively taller + relatively shorter pairs of siblings was studied
  - Criteria was met
    1. Heritable and positively genetically correlated – Siblings resembled each other's heights more than unrelated individuations
    2. Negatively phenotypically correlated
  - Height determined offspring output
    - Shorter siblings → Females had more offspring BUT males had less
    - Taller siblings → Males had more offspring BUT females had less
  - And conflict remained unresolved
    - Taller offspring → Sons more reproductively fit
    - Shorter offspring → Daughters more reproductively fit

- **Intralocus conflict is also seen in offspring fitness of crickets**
  - Predictions – (1) High quality males → High quality sons but low quality daughters (2) Vice versa
  - Experimental set up – Reproductive success (i.e. mate attraction + offspring output) of males was measured
  - Results – In line with predictions
- **Consequences of intralocus conflict**
  - Constraint to (/slow down) evolution – Trait under 'tug of war' → Unable to evolve towards M or F optimum
  - Evolution will attempt to resolve this through:
    - Evolution of sex specific gene expression/recruitment of genes to the sex chromosomes → Taken out of conflict (e.g. Evidence in *Drosophila* – Rate of gene recruitment to male Y chromosome is 10x higher than gene loss)
    - Evolution of new sex chromosomes

<u>Interlocus conflicts (might drive co-evolutionary arms race)</u>

- **To demonstrate this conflict is happening we must:**
  1. Find a sex specific (offensive) trait that has benefits for one sex BUT is costly for the other
  2. Find the paired (defensive) trait in the opposite sex
  3. Show the traits evolved in response to each other
- **E.g. Extreme conflict – Sexual cannibalism in garden mantis**
  - Females eat males after mating → An evolved self-sacrificial behaviour IF males are able to mate with high quality females (detected by pheromonal cues) resulting in greater offspring output
  - **Experiment** – Measured female quality (# eggs produced) and attractiveness to males
  - **Results** – Attractiveness increased from Poor → Medium → Good quality BUT very poor quality females appeared extremely attractive to males, despite offering reduced male fitness gain
  - **Explanation** – Poor quality females mimic high quality pheromones to manipulate males to mate with them, overcoming this trade-off without substantial investment
- Interlocus conflict that results by deviation from monogamy has been described as **three way tug of war**
  - (1) + (2) – Males facing sperm competition with each other to produce the most offspring → **Offensive** traits evolved to compete may cause collateral damage to the female
  - (3) – Females also trying to produce the most offspring → Evolves a **defensive** trait to prevent damage caused by competing males
- **Parker (2006) developed a theory that this could result in a sexually antagonistic co-evolutionary arms race**
  - (1) Male offensive trait arises which is costly to female
  - (2) Female responds by investing more greatly into defensive trait
  - Male vs male trait (offensive) causes reducing in female fitness → Female counter-adaptation then reduces male fitness → Further exaggeration of offensive trait → etc – Escalating costs for Ms + Fs
  - Eventually results in a crash, circling back to starting the conflict again (after M or F threshold is exceeded)
  - Vm = max investment for male, Vf = max investment for female
  - In the hypothetical scenario, males are able to withstand more costs than females (Vm > Vf)





- **Evidence of sexually antagonistic co-evolutionary arms race in *D. melanogaster***
  - Male production/transfer of sex peptide:
    1. Reduces female re-mating (→ reduced sperm competition → increases male's offspring output, BUT effects aren't permament)
    2. Increases female egg laying rate (increases male + female offspring output)
    3. Reduces female lifespan

- **Experimental set up** – *Drosophila* tissues analysed – (a)Testis – Producing seminal fluid and sperm (b) Ovaries – Producing female reproductive tract proteins and oocytes
- **Obvious pattern** – Male conflict (e.g. sperm competition) are driving high evolutionary rates in tissue specific gene expression in testis, seminal fluid, and sperm BUT the female genome is not matching this rate of evolution
- Sex peptide has very little homology amongst species, but sex peptide receptor is ancient – Males have hijacked this system (which previously had a different use) for use in sexual conflict

- **Has interlocus conflict driven speciation?**
  - Possibly but hard to measure – If conflict can drive evolution fast enough, it will result in speciation more quickly
  - Across all species of *Drosophila,* some are hermaphrodites but some have separate sexes
    - ➢ Hermaphrodites are predicted to have arisen at least twice independent from most species that have 2 sexes
  - If forced to, inter-species (heterospecific) mating will occur BUT has been demonstrated to be more harmful (i.e. reduced reproductive output, sterilise maternal individuals) than conspecific mating
    - ➢ Different species are under different evolutionary conflicts – Evolved defences are only compatible with male offensive traits of their own species
  - Studies demonstrate hermaphrodites are more negatively affected (i.e. offspring output/lifespan) than females
    - ➢ Ability to self-fertilise → Reduced sexual selection to maintain defences against males
  - Reproductive isolation is reinforced by assortative mating to avoid this cost
    - ➢ Heterospecific matings only occur if the individual is forced to
    - ➢ Assortative mating = A form of sexual selection in which individuals with similar genotypes and/or phenotypes mate with one another more frequently than would be expected under a random mating pattern
  - Assortative mating → Reduced negative effects of heterospecific mating → Reinforcement of (/rapid) speciation

<u>Summary on interlocus conflict</u>

- Evidence must demonstrate
  - A sex-specific trait that has benefits for one sex (offensive) but is costly for the other
  - The counter adaptation (defence) in the opposite sex, and that the traits evolved in response to each other
- Might result in evolutionary arms race
- Proposed consequences/predictions of causing evolutionary arms races
  - Increased rate of evolution
  - Drives/reinforces speciation
- Examples given appear clear-cut BUT is in fact incredibly difficult to demonstrate in the natural world because we can often only take a 'snapshot' of evolution
  - Finding both traits and demonstrating they're evolving in response to each other is difficult

<u>Sexual conflict summary</u>

- Males and females often have different fitness optima for the same traits – This leads to conflict
- Intragenomic conflict occur over traits expressed by both sexes → Could drive sex-biased expression and constrain evolution
- Intergenomic conflicts occur over traits expressed by one or the other sex → Could drive evolutionary arms races and faster rates of evolution
- There is limited evidence supporting the phenomenon of sexual conflict and its effects on evolution BUT growing interest in the field

<u>Reading</u>

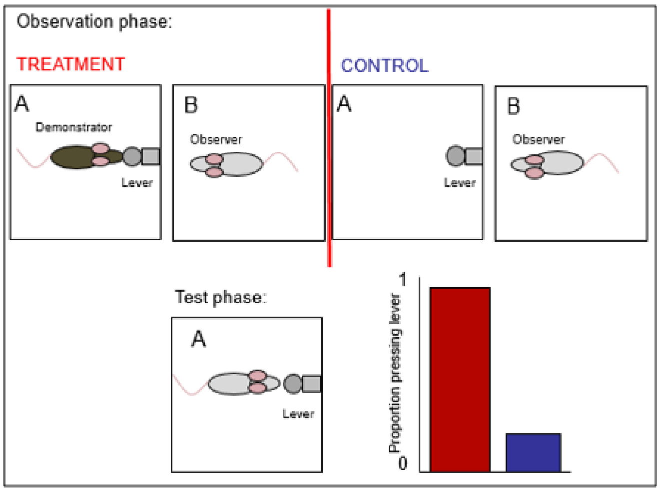
- Davies, Krebs and West An introduction to Behavioural Ecology 4th Ed pp 209-218
- Fricke, C., A. Bretman, and T. Chapman. 2010. Sexual Conflict. Pp. 400-415 *in* D. F. Westneat, and C. W. Fox, eds. Evolutionary Behavioral Ecology. Oxford University Press, Oxford.
- Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe 2003 TREE 18:41-47
- Bonduriansky and Chenoweth 2009 TREE 24:280-288

<u>EXAM ADVICE</u>

- ANSWER QUESTIONS WITH LECTURE CONTENT EXAMPLES – Further reading from other lectures is less crucial
  - Try to demonstrate increased depth to examples given – see Reviews (cited in lectures/reading lists)

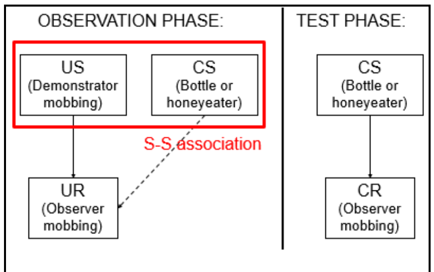
Step 2 – Identify pattern consistent with the process

- First question – Does the animal have the capacity to learn? (chapter 3 intro)
  - Addressed through traditional demonstrator-observer experiment
- Hypothetical (poorly designed) rat experiment
  - Basic pattern – An observer watching a trained demonstrator press a lever to release food is more likely to press the lever in the test phase than the control observer
  - Consistent with imitation BUT also with plausible alternatives that need to be ruled out



Step 3 – Recognise plausible alternatives

1. **Social facilitation** (chapter 4.1.5)
   - The mere presence of a (conspecific) demonstrator affects the observer's behaviour (e.g. increased activity levels) in a way that increases its probability of finding/pressing the lever randomly, thereby accidently discovering the yielded food reward → Repeat behaviour
2. **Stimulus enhancement** (chapter 4.1.1) → Can lead onto further learning
   - Observation of a demonstration (or its products) exposes the observer to a single stimulus (e.g. the lever), after which it is more likely to interact with that stimulus (in the test phase), thereby investigating the lever and accidently pressing it to discover the yielded food reward → Repeat behaviour
3. **Local enhancement** (chapter 4.1.2) – A debatably separate sub-set of (2) → Can lead onto further learning
   - After or during a demonstrators presence, or interaction with objects (e.g. lever) at a particular location, an observer is more likely to visit or interact with objects at that location, thereby investigating the area surrounding the lever and accidently pressing it to discover the yielded food reward → Repeat behaviour
4. **Observational conditioning** (chapter 4.1.3) – A sub-set of stimulus-stimulus learning (e.g. blackbird example)
   - Observation of a demonstrator exposes the observer to a relationship between stimuli (e.g. lever + food reward), causing it to learn the association between them during the observation phase, thereby being more likely to investigate the lever in the test phase and accidently press it to discover the yielded food reward → Repeat behaviour



Curio (1988)

5. **Response facilitation** (chapter 4.1.4)
   - Presence of the demonstrator performing an act (e.g. paw pushing action) increases the probability of the observer repeating the same act (in any context), without any association made between the act and the lever/food reward – When in the test phase, the observer is more likely to perform that act on the lever to release food, thereby learning the association → Repeat behaviour
6. **Emulation** (chapter 4.1.8) – Arguably a type of imitation BUT often distinguishable
   - After observing a demonstrator interacting with objects (e.g. pushing lever with paws) in its environment, an observer is more likely to perform any action (e.g. using face/feet/tail) that brings about a similar effect on those objects – Observer is emulating an action, not imitating it

Back to step 1 – Redefining imitation more specifically (chapter 4.1.6)

- Many researchers think 'imitation' should be defined as a **novel behaviour** to distinguish it from the plausible alternatives
- BUT this is not such a clear-cut concept
  - It could be argued that (1) Every action an animal performs is novel (2) No action an animal performs is novel – It is just a sequence of familiar actions that is novel, not the individual components
- Imitation must be defined in a way that eliminates this problem