

In this chapter, we'll use case studies of adaptation in signalers and receivers to discuss a variety of approaches to asking and answering questions about the processes involved in the evolution of behavior. The main "take-home" messages from these studies are

1. Because the conditions necessary for natural selection to occur are widespread, it's reasonable to start with the assumption that complex traits (including behaviors) have some adaptive function and have, therefore, evolved (at least in part) by natural selection.
2. However, we must remember that not all traits are adaptive, and that even traits that serve a current adaptive function may have had quite different functions in the past. Adaptive hypotheses about both current and past function must be carefully constructed and rigorously tested against a variety of alternative adaptive and non-adaptive hypotheses.
3. The adaptationist approach has been very useful for identifying and addressing "Darwinian puzzles" – behaviors (and other traits) that seem initially to be maladaptive and consequently difficult to explain in traditional ways.
4. The ability of "illegitimate signalers" to exploit otherwise adaptive responses of individuals to specific signals illustrates the kinds of trade-offs that constrain selection and, consequently, require us to seek more subtle and complex explanations than we might initially propose.

CHAPTER 8: ADAPTATION IN SIGNALERS AND RECEIVERS

- A. The meaning of adaptation – important points to remember:
1. Adaptation can be defined differently by different people – it's important to clarify which meaning is being used (current adaptive function vs. historical adaptive origin)
 2. Regardless of one's preferred definition, all evolutionary biologists recognize that complex traits have complex histories; to understand those histories fully, we need to take into account that:
 - a. current adaptive function may or may not be original function
 - b. not all traits are adaptive – some may be

- i. adaptively neutral – because
 - a) they're neutral consequences of adaptive traits
 - b) the organism's environment has changed such that the trait no longer has adaptive value
 - ii. somewhat maladaptive – because
 - a) the environment has changed and selection hasn't "caught up"
 - b) appropriate genetic variation for improvement doesn't exist
 - c) they're consequences of other, more adaptive traits (benefit from the adaptive trait exceeds cost of poorly adapted trait)
 - d) they're adaptive in most circumstances and maladaptive in just a few
 - c. selection itself is a complex process that can be strongly influenced/affected by
 - i. constraints imposed by organism's current developmental mechanisms, anatomy, physiology, etc. (e.g., sensory exploitation)
 - ii. historical contingency (chance) – for many environmental "problems", multiple adaptive "solutions" may be possible; which one is "picked" may be a function of chance (which set of favorable mutations arose first) – e.g., having disruptive camouflage is undoubtedly adaptive for young of many species, but precise pattern probably has more to do with chance than anything else
3. Because of these complexities, it's important to remember that hypotheses about the adaptive benefits of a trait are hypotheses that must be tested
- a. against other adaptive hypotheses
 - b. against non-adaptive hypotheses
- B. Testing adaptive hypotheses #1: why is singing in birds largely restricted to males?
- 1. Non-adaptationist hypothesis (just for example): females fail to sing because the development of female reproductive anatomy, physiology and behavior disrupts the development of the song system
 - a. if this is correct, would predict that no (or very few) bird species have elaborate female song – prediction is not met

- b. because many species have elaborate female song, song systems and female anatomy, physiology, behavior not automatically incompatible
 - c. note, though, that this reasoning assumes comparable developmental systems in all species – needs further testing
2. Adaptationist hypothesis (not the only possibility): males sing more than females in most species because males receive more fitness benefits from singing than do females. Hypothesized fitness benefits (not mutually exclusive) and tests are
- a. Singing enhances male mating success (by making males more attractive to females)
 - i. **prediction/test #1:** females are attracted to male song – playback studies demonstrate females more attracted to nest boxes with taped songs than to nest boxes with no song
 - ii. **prediction/test #2:** monogamous males will stop singing once a mate has been acquired; polygynous males will continue singing (trying to attract additional mates) after one mate has been acquired -- confirmed in some species, but not tested extensively
 - iii. **prediction/test #3:** in species with variation among males, females should respond to variation in male song (should be able to detect, evaluate differences) – in starlings, best predictor of male success in pairing with females is song complexity
 - b. Singing benefits males by better enabling them to defend territories from rival males
 - i. **prediction/test #1:** song alone should repel intruders from territories – in white-crowned sparrows, new males are slower to enter “vacated” territories with taped song than vacated territories without song
 - ii. **prediction/test #2:** muted males should be less able to defend territories than non-muted males – territory invasion increased following operation to mute males (and muted males eventually lost their territories), although not in sham-operated birds

- c. Singing benefits males by allowing them to advertise ability to defend mate(s) from “sneak copulations” by rival males
 - i. **prediction/test #1:** song rate peaks when females are most fertile (when risk of loss due to sneak copulations is greatest) – in some species (e.g., great tit), frequency increases with fertility
 - ii. **prediction/test #2:** song quality (number of songs, duration of singing) should increase with male’s physical condition – European blackbirds given supplemental food sing longer the next day than on days following no supplemental food
 - iii. **prediction/test #3:** visits by intruder (rival) males will decline with song quality
 - a) in European starlings, nestboxes with taped song attracts males, contrary to prediction
 - b) but, more males visited boxes with simple songs than boxes with complex songs – meeting the prediction
3. Summary:
- a. In many species, song provides current fitness advantage to males – although the “form” of that advantage may vary among species – supporting the “male fitness advantage” hypothesis for why males, rather than females, sing in most birds.
 - b. In this case, it’s reasonable to suppose that any one of these current adaptive functions could have been original adaptive function of bird song, although we can’t specify which one it might have been
 - c. What kinds of studies could you do on species in which females produce elaborate songs to shed further light on this question?
- C. Testing adaptive hypotheses #2: are song dialects adaptive ?
- 1. Non-adaptive hypothesis: differences in dialects arise as a “side-effect” of song learning mechanisms
 - a. Under this hypothesis, divergence of dialects is the result of “accidental” or

- random variation in songs among regions
- b. **prediction/test:** if divergence is random and has no fitness consequences, females should exhibit no preference for own song dialect over others –
 - i. female cowbirds prefer songs of own subspecies
 - ii. therefore, males gain fitness advantage by having “proper” dialect
 - iii. prediction not met – but how strong is this test?
2. Adaptive hypotheses:
- a. Dialects allow males to communicate place of origin to females – allowing females to choose mates whose genetic background matches their own and is suitable for their own region
 - i. **prediction/test #1:** females should prefer dialect that matches their father’s – no such preference in one population of white-crowned sparrows
 - ii. **prediction/test #2:** song dialect in males should be unable to change natal dialect (if it changed, it wouldn’t be a reliable indicator of place of origin) – not met in white-crowned sparrows.
 - b. Dialects allow males to communicate with neighboring males
 - i. **general prediction/test #1:** in species with one or a few song types, males should learn and match songs to those of their neighbors, regardless of their place of origin (matching increases ability of neighbors to “understand” message from song) – met in white-crowns and other species
 - ii. **general prediction/test #2:** in species with variable repertoires (multiple song types), males should “reply” to songs of neighbors with matching song types (similar to above, but matching is facultative choice among available song types, rather than learning one matching song type) – in song sparrows, male chooses song from own repertoire that best matches neighbor’s songs
 - iii. **general prediction/test #3:** in species with separate “for female” and “for male” songs, should get more variability and more complex learning systems in “for male” songs (to allow neighbor matching) than in “for female” songs –

met in chestnut-sided warblers:

- a) “for female” song is learned early and shows little variability among males
- b) “for male” song is learned over a longer period of time, can be modified throughout the bird’s lifetime, and varies among locations
- c. More specific version of male-male communication hypothesis – males are communicating status as neighbors or strangers. This would be adaptive if, for example, strangers are more likely than neighbors to challenge the territory holder.
 - i. **prediction/test:** territorial males should react more strongly to playback tapes of strangers than of neighbors – met in lots of territorial species (not just birds)

3. Summary:

- a. Although we haven’t reached consensus on the particular case of white-crowned sparrow dialects, we do have evidence that, for at least some species, differences in song among males serves current adaptive function(s) in some species.
- b. Do these studies shed any light on the historical sequence of dialect acquisition? Do we have any direct evidence of fitness benefit?

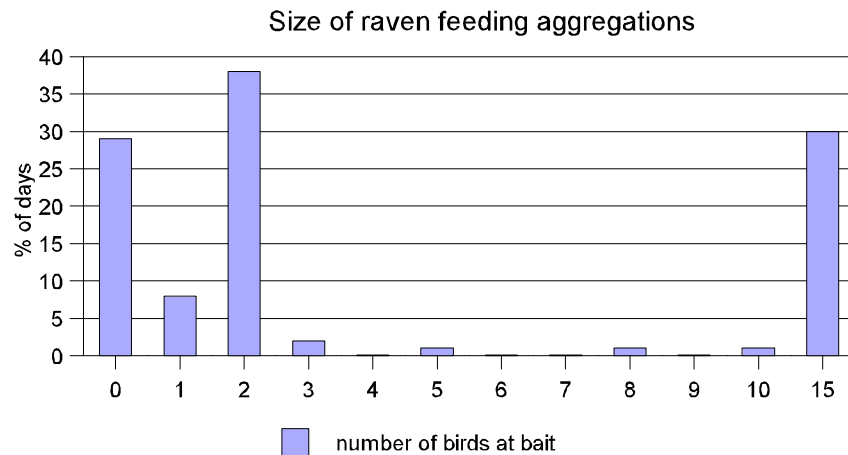
D. Adaptationist approaches and Darwinian puzzles: if we make the assumption that complex behaviors serve a current adaptive function (whatever their full history might be), we can identify interesting behaviors that appear to violate this assumption – they appear to result in a fitness loss rather than a fitness gain.

- 1. Darwinian puzzle #1 – sharing in ravens, studied by Bernd Heinrich (see his book, Ravens in Winter for a great description of this work; some of it is also discussed in your readings text).
 - a. natural history:
 - i. Ravens belong to the family Corvidae, along with crows and jays.
 - ii. In Maine (where Heinrich studied them), ravens are fairly sparsely distributed over large areas.

- iii. In winter, ravens scavenge carcasses – which are themselves limited outside hunting season.
- iv. One day, Heinrich saw a group of ~ 15 birds feeding on a moose carcass. He was puzzled when he saw and heard some birds calling – apparently to attract other individuals to the carcass. This was puzzling, because sharing scarce food resources seemed maladaptive (the more adaptive behavior would be to keep the food secret for oneself).
- b. Non-adaptive hypothesis: aggregation simply a function of solitary birds all finding the same carcass
 - i. **prediction/test #1:** birds are densely enough populated to “find each other” and to find carcasses quickly and efficiently by chance – inconsistent with population density, distribution
 - ii. **prediction/test #2:** calls don’t serve to attract other birds – but taped calls do attract other ravens, so prediction not met
- c. Adaptive hypothesis #1: calling birds are parents calling offspring (increasing their own fitness by helping kin)
 - i. **prediction/test #1:** raven pairs have relatively large numbers of offspring (to account for large number of birds aggregated) – no, have maximum of 6 offspring.
 - ii. **prediction/test #2:** birds are close relatives – DNA studies demonstrate that birds are unrelated.
- d. Adaptive hypothesis #2: calling birds are trying to attract large mammalian predators (coyote, bear) to open carcass
 - i. **prediction/test:** given new, “unopened” carcass, birds should call – tested by placing goat in various locations over several weeks – even when birds found the carcass, they didn’t call.
- e. Adaptive hypothesis #3: noticed that birds very cautious when initially approaching carcass -- proposed that calling birds are trying to “dilute the risk” of predation – either by a “not dead yet” animal, or by other scavengers who

might find the carcass. The caller gets diluted risk, attracted birds get lots of food for relatively little gain in risk.

- i. **prediction/test:** once a group has assembled and start feeding, calling should stop
 - ii. observed groups feeding on variety of carcasses (provided by him) – not met – birds keep calling even after feeding begins
- f. Adaptive hypothesis #4: after many, many hours of observation and experiments with different carcasses, noted that
- i. whenever one or two birds were at a bait, they were silent; calling only happened when 3 or more birds were present.
 - ii. knew that older adult ravens are territorial and defend territories year-round
 - iii. knew unmated younger birds usually traveled singly over large distances looking for food
 - iv. knew that when single young birds tried to feed on carcasses in a territory, the territorial pair defends the food (driving subordinate away)
 - v. so, proposed that callers were juveniles attempting to “gang up on territory owners” – caller is trying to attract enough juveniles to overwhelm territory owners. This benefits caller (who otherwise wouldn’t get any food) and other singletons, who share caller’s food
 - vi. **predictions/tests:**
 - a) resident territory owners should never yell to advertise food – met
 - b) nonresidents should yell when they find food – met
 - c) yelling should bring lots of nonresidents to ‘attack’ carcass – met
 - d) resident pairs should be unable to defend carcasses in their territories from groups of juveniles – met
 - e) carcass should be fed upon either by pairs or by mobs – rarely by one, or by small number greater than 1 – met:



- f) Interestingly, this finding also helped explain adaptive significance of group nocturnal roosting in this (and potentially other) species – nocturnal roost site seems to act as “information exchange center” for subordinates.
- g. Conclusion: yelling is an adaptation for gaining access to food resources in subdominant individuals – the “cost” of sharing food is outweighed by the benefit of having access to carcasses.
2. Darwinian puzzle #2: Ryan’s Tungara frogs
- a. As we’ve already discussed, male Tungara frogs have 2-part call that’s attractive to females. But males only use the 2-part call occasionally. If the 2-part call is adaptive, this would seem to be maladaptive.
 - b. Hypothesis = 2-part call increases risk of predation by bats (genus Trachops), so that under some circumstances, cost of 2-part call outweighs its benefit
 - i. **prediction/test #1:** bats are attracted to frog calls – met in playback experiments (bats prefer speakers playing songs to silent speakers)
 - ii. **prediction/test #2:** bats prefer whine-chuck to whines alone – met
 - iii. **prediction/test #3:** tendency of males to produce whine-only calls should increase with predation risk – males alone or in small groups are more likely to produce whine-only calls than males in larger groups – met

- c. Conclusion: flexibility to produce both kinds of calls is adaptation for acquiring mates while minimizing predation risk.
3. Darwinian puzzle #3: exploitative receivers and illegitimate signalers
 - a. Example above illustrates common phenomenon of predator species exploiting communication signals in prey to locate prey.
 - b. We can also find many examples of the reverse: individuals use specific signals to deceive other individuals, often in order to prey upon them. E.g.'s include
 - i. Female Photuris fireflies mimic "reply flash" of females in genus Photinus, luring Photinus males close enough to grab, kill and eat.
 - ii. Male Portia fimbriata spiders mimic males of Euryattus sp., luring females out of web and preying on them
 - iii. More generally, many predatory spider spp. lure web-builders by mimic vibration patterns of insects trapped in webs
 - iv. Angler fish use lures
 - v. some male garter snakes produce female sex pheromones, potentially distracting other males from actual females as females emerge
 - c. Both phenomena are puzzles – signal generators or signal receivers seem to be engaging in maladaptive behavior.
 - d. Two general hypotheses usually proposed for such puzzles:
 - i. **novel environment hypothesis**: maladaptive response is the product of a proximate mechanisms that was adaptive in the past, but is not now because the environment has changed – usually reserved for relatively recent human modification of the environment
 - ii. **exploitation hypothesis**: maladaptive response is caused by proximate mechanism that is adaptive most of the time for most individuals, but that is exploited occasionally.
 - a) idea is that per-individual fitness cost of being exploited is less than the benefit gained by responding to the signal
 - b) reason is that the risk of being exploited is fairly low – most of the time,

the signal is “honest”

- c) general prediction for this hypothesis is that deception exploits a response that has a clear adaptive value under most circumstances – so that individuals ignoring the signal pay a high fitness cost
- d) but, although this is very plausible, it may be hard to test – how would you attempt to test this prediction in fireflies, garter snakes?