1. For the remainder of the semester, we'll be examining different categories of behaviors. In addition to general surveys of the range of behavior found within each category, we'll pay particular attention to historical analysis, continuing to refine our understanding of how historical analysis is actually done.
2. In this chapter, we'll survey behavior related to predation by following the stages through which predator-prey interactions proceed:

   detection –> attack –> capture –> consumption
3. You should be able to describe different strategies used at each stage, although we'll only cover a few in detail in lecture (we'll look in depth at the ones that offer good opportunities for studying methods, theory).
4. We'll also add some refinement and new techniques to our list of "how to" study adaptation:
   a. we'll distinguish between demonstrating fitness advantage and demonstrating performance advantage, which is often "substituted" for fitness advantage in tests of adaptive hypotheses
   b. we'll introduce a specific and powerful form of the comparative method for testing adaptive hypotheses
   c. we'll formalize the way we think about the costs and benefits of different kinds of behavior into **optimality models** that let us predict how behavior should vary with environmental or other conditions

CHAPTER 9: ADAPTIVE RESPONSES TO PREDATORS

A. In theory, to support hypotheses about the adaptive value of behavior, we need to be able to demonstrate that some variants of the behavior produce fitness benefits compared to other forms of the behavior (this holds for other kinds of traits as well).
   1. Unfortunately, demonstrating fitness benefits can be extremely difficult: in the strictest sense, we would need to be able to measure the lifetime inclusive fitness of many individuals – which, in turn, would mean being able to count direct offspring, offspring of sibs, etc., over at least two generations.

2. Because that is often impossible, we often rely on "proxies" or "substitute" measures of fitness: rather than demonstrate that a particular variant increases fitness, we demonstrate that it provides some kind of **performance advantage**.
    a. Means that an individual is able to accomplish some important life task better than others in the population.
    b. We reason that saving time or energy, or being better able to acquire critical resources, will be translated into fitness benefit.
    c. Performance advantages are often much easier to demonstrate than fitness advantages; although they're very important components of ultimate analysis, it's important to recognize the difference between a performance advantage and a fitness advantage
3. The distinction between a fitness advantage and a performance advantage is not necessarily easy to draw
    a. Alcock's Table 2 p. 294 is one scheme (his "indrect measures of reproductive success" are performance advantages)
    b. I prefer the following (but this is a matter of personal preference!):
        A. Fitness advantage (= direct reproductive benefit)
            1. Number of young over individual's lifetime that reach reproductive maturity
            2. Number of young produced during a single breeding season that reach reproductive maturity
            3. Number of young produced during a single breeding season that reach independence
            4. Number of young born/hatched during a single breeding season
            5. Number of fertilized eggs produced
        B. Performance advantage (= assumed to translate into fitness advantage)
            1. Number of gametes produced

2. Number of mates acquired
3. Number of copulations
4. Predator avoidance
5. Food acquisition
6. Possession of living space
7. Efficiency of locomotion or other activities

C. In this chapter, we'll also introduce and use new tools for developing and testing hypotheses about the adaptive nature of behavior:

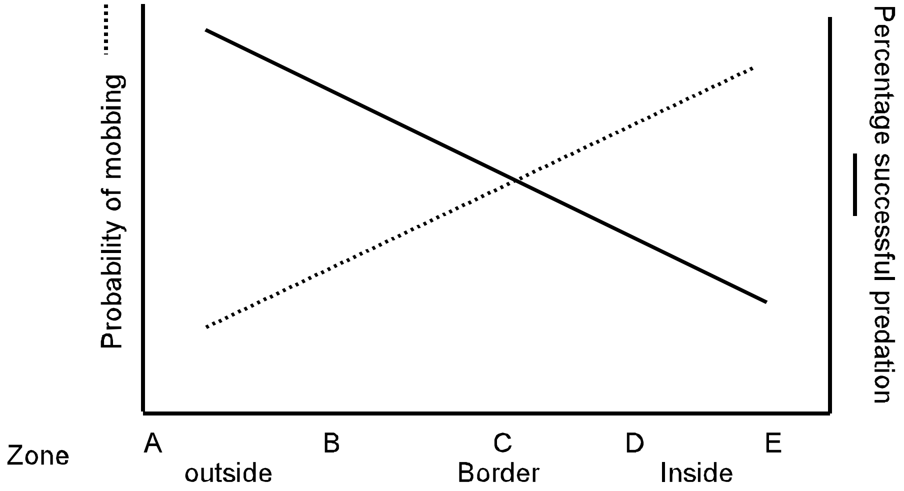
1. The "classic" **comparative method**
    a. this allows us to distinguish between two alternative hypotheses for the presence of a behavior in a given species:
        i. the behavior is an adaptation to that species' ecological setting
        ii. the behavior is a neutral trait inherited from an ancestor
    b. the method involves comparing the species in question with
        i. a close relative whose ecological setting is different
        ii. a non-relative (or more distant relative) whose ecological setting is similar
    c. we predict that, if the behavior is an adaptation, it should be
        i. **not present** it in the related species with **different ecology**
        ii. **present** in the **ecologically similar**, but distantly related species
    d. similarly, if the behavior is a neutral trait inherited from a common ancestor, it should be
        i. present in relatives in spite of ecological differences
        ii. not present in non-relatives, in spite of ecological similarity
2. **Optimality models**
    a. These are models (verbal, graphical, mathematical) based on the idea that, among the variant behaviors available, selection will favor those that maximize benefits relative to costs (usually measured in terms of specific performance advantages, often measured in units of energy).

- b. They are especially useful when costs and benefits vary across environmental or other conditions – they allow us to predict how the "optimum" behavior will vary with those conditions
- c. Two general forms of the models:
    - i. Optimality models per se: used when variation in costs/benefits are a function of abiotic conditions in the environment
    - ii. **Game theory** models: used when variation in costs/benefits are a function of the interaction of two or more individuals
    - iii. we'll be looking only at the former in this chapter – we'll look at game theory in other chapters

D. Adaptations to avoid detection

1. **Mobbing** in black-headed gulls (and other species)
    - a. Black-headed gulls form large breeding colonies in open, grassy habitats
    - b. When potential predator appears, adults begin with groups of loud cries; if intruder persists, groups of gulls fly at it, defecate on it, etc.
    - c. What is the adaptive benefit? Because the behavior occurs primarily during the breeding season, obvious hypothesis is that gulls are distracting predators from young
    - d. **Test #1**: observation – if hypothesis is correct, should see that mobbing behavior prevents potential predators from finding eggs, young – met
    - e. **Test #2**: experiment
        - i. If mobbing protects eggs, young, the degree of protection should be proportional to the intensity of the mobbing
        - ii. Kruuk and colleagues tested this prediction by placing hens eggs along a transect from inside to outside the border of the colony – measured probability of mobbing and percentage of successful predation attempts:
            - a) mobbing rates increased toward center of colony
            - b) predation rates decreased as mobbing rates increased

c) (note important to demonstrate both!):

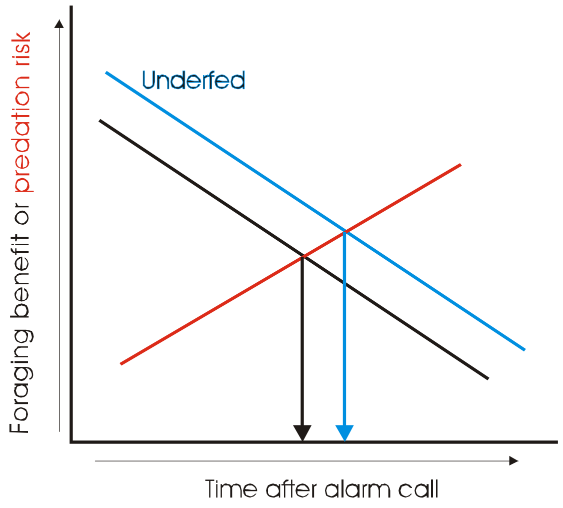


f. **Test #3**: comparative method
   i. The mobbing response “makes sense” for a species that nests in large numbers in fairly open habitat, because this makes eggs/young vulnerable to substantial number of potential predators
   ii. If this is the case, then we should find that:
      a) related species of gulls nesting in habitats less vulnerable to terrestrial predation should not exhibit the behavior
      b) unrelated species in similar habitats should demonstrate mobbing
   iii. Kittiwake gulls nest on cliffsides where terrestrial predation is virtually nonexistent – they don’t exhibit the behavior – **prediction met**
   iv. many unrelated bird species (even mammal species – clearly only distantly related!) with colonial nesting and vulnerability to predators also mob (e.g., swallows, ground squirrels) – **prediction met.**

        v. Note again the importance of understanding systematics, natural history!

2. **Cryptic behavior:**
    a. Huge number of species combine cryptic colors/patterns with cryptic behavior
        i. cryptic color/pattern = any of a number of colors and patterns that blend into background, obscure outlines, hide shadows, etc.
        ii. cryptic behavior = any behavior that minimizes visibility
    b. E.g., Catacola moths:
        i. Wings have dark horizontal stripes on pale background
        ii. Given choice, moths
            a) selects birch over trees as roost sites
            b) orient bodies head-up on birch trunks, aligning stripes on wings with dark lines on the birch bark
        iii. Jays taught to peck at moths in photographs
            a) "saw" moths 10-20% less often when moths on birch than on other backgrounds
            b) overlooked moth more often when oriented head-up than in other positions
        iv. neat question: how does moth (and other species) "know"
            a) which backgrounds are safest
            b) which way to orient
    c. Cryptic behavior generally involves being still or otherwise hidden – which means that individuals engaging in it are bearing a cost in the form of time lost for other activities (feeding, mating, etc.).
        i. Those costs may vary among individuals based on physiological condition, e.g., or across environmental conditions
        ii. we can use optimality models to understand (predict) how behavior should vary (among individuals or across range of environmental conditions)

d. E.g. #1: Belding's ground squirrels
  i. Squirrels diurnal, forage in open grassy habitats where they're subject to predation by lots of different predators
  ii. Individuals within populaiton use alarm calls to warn each other about potential predators; typical response to alarm call = hiding in underground burrow
  iii. time in burrow = time not spent feeding
  iv. cost of time lost for feeding should vary among individuals depending on their nutritional status: well-fed squirrels have less to gain from additional feeding time than do underfed squirrels:



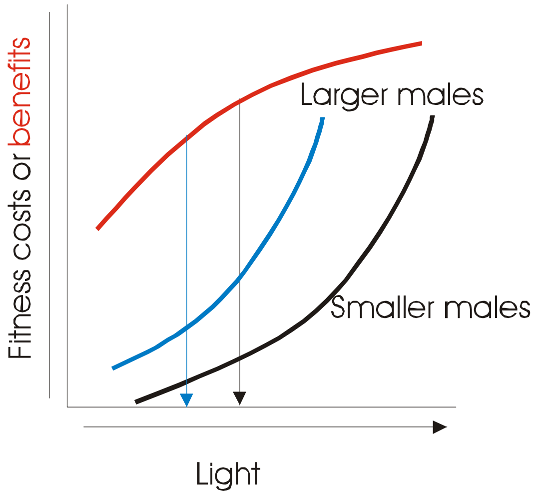
  v. Therefore, predict that underfed squirrels should stay above ground longer after alarm calls than well-fed squirrels – tested and confirmed by Bachman.

e. E.g. #2: Trinidadian guppies
  i. These small fish have been extremely important model species for ecological and behavioral studies:
    a) live in small streams in Trinidad

- b) within individual stream system, can get range of ecological conditions (speed of water flow; substrate; number, kind of predators; etc.)
- c) within stream system, find differences among populations in all kinds of behaviors correlated with differences in ecology
- d) differences range in degree to which “caused” by differences in genetics, environment
- e) range of studies suggest that individuals are highly sensitive to presence of predators; predation risk

ii. In populations with relatively low (but not nonexistent) predation risk, females prefer big, brightly-colored males with vigorous courship displays

- a) cost to male = risk of predation by visually-hunting predatory fish
  - 1) cost should increase with light intensity
  - 2) for all light intensities, costs should be greatest for larger males:



- b) optimum behavior = benefits maximally exceed costs: predict that
  - 1) males should court most vigorously at moderate light intensities (at low light, not visible to females; at high light, too visible to predators)

        2) over all light intensities, small males should court more vigorously than large males; difference should be greatest at high intensity
        3) predictions met (see fig. 13).

E. Adaptations to reduce attack rate
    1. Many species have physical (e.g., spines, bristles) and/or chemical defenses that deter predators through pain, noxious taste, etc.
    2. Many species “benefit” by “advertising” noxiousness to potential predators = adopt **aposematic** (warning) **coloration** (and, for some, behavior).
        a. In general, aposematic colors are bright, vivid – to “stand out” against background
        b. common combinations = red/orange/yellow + high contrast black/white
    3. Aposematic colors “make sense” if we consider current function:
        a. in aposematic species, all individuals have same color pattern (and many have convergent patterns)
        b. predators will learn to avoid aposematically-colored individuals through operant conditioning
        c. because all individuals within the species have same pattern (and many have convergent patterns), chances of any one individual being taken by naive predator are very low
    4. But, this begs the question – how could aposematism have evolved originally?
        a. Current benefit is a function of many individuals having same color pattern
        b. Originally, the aposematic pattern must have been restricted to relatively few individuals
        c. Those few individuals, because of their color pattern, would have been more visible to predators
        d. And, because most individuals wouldn’t share the color pattern, predators wouldn’t have much opportunity to learn to avoid the pattern
    5. Several mechanisms have been proposed to account for origin of aposematic

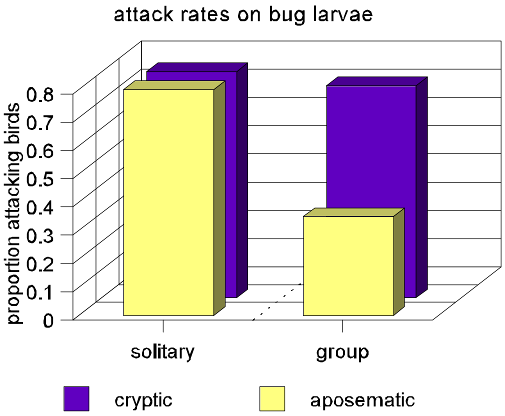
coloration; each has been supported by experimental evidence in different groups of species

- a. **kin selection**: individuals benefit via benefit to close relatives
  - i. Any mutation giving rise to incipient aposematic coloration would be shared by close relatives (clones, sibs, half-sibs, etc.)
  - ii. An individual's fitness could remain high in spite of being killed by predator if predators learned to avoid eating similarly-colored individuals – predator would be avoiding kin, who share that individual's genes
  - iii. If aposematic colors increased the speed with which predators learned to avoid that particular kind of prey, and given relatively large, gregarious kin groups, selection would then favor the aposematic coloration.
- b. **individual selection**: the presence of incipient aposematic coloration benefits individuals through one or more of the following:
  - i. **decreased risk of consumption** due to noxiousness: predator captures aposematically-colored individual, but noxious taste increases that individual's chance of being released before being killed (this happens in monarch butterflies)
  - ii. **decreased risk of attack** due to novel appearance: because prey item looks very different from "normal" prey, evokes innate avoidance response (**neophobia**) on part of potential predator
  - iii. (to think about: could this be a form of sensory exploitation?)

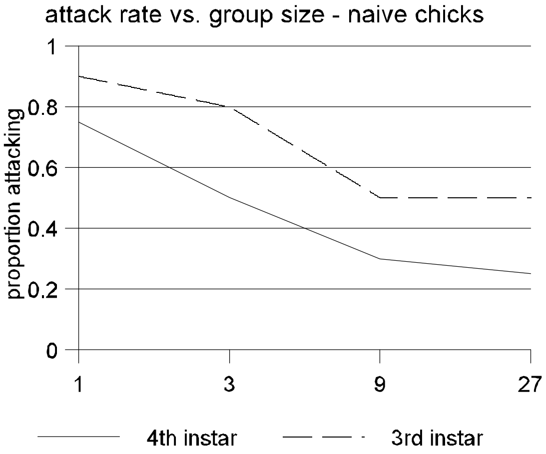
6. Many species of aposematic insects are also highly gregarious (cluster in large groups) – is this adaptive, and, if so, why?
   - a. three possibilities have been suggested:
     - i. according to the kin selection model, gregariousness is a pre-requisite for the evolution of aposematic coloration
     - ii. gregariousness could be favored in aposematic species if it increased the speed with which predators learned to avoid noxious prey

- iii. gregariousness could be favored in aposematic species if it increased the signal value of the coloration – i.e., simply reduced the frequency of attack (by heightening, e.g., the neophobic response) even for naive predators
- b. Birgitta Sillen-Tullberg has examined these hypotheses in a series of analyses
  - i. evaluated the kin selection hypothesis by doing a phylogenetic analysis of butterflies (where larvae are aposematic -- see web resources):
    - a) the kin selection hypothesis predicts that, whenever aposematism evolves, it is preceeded by gregariousness
    - b) mapped the distribution of aposematism and gregariousness onto cladograms of 10 lineages of butterflies. Combining results of all analyses, she found
      - 1) 3 cases in which aposematism and gregariousness appeared to originate together (i.e., couldn’t place one before the other)
      - 2) 15 cases in which aposematism preceded gregariousness
      - 3) 9 cases of aposematism in lineages with solitary larvae
      - 4) 0 cases of gregariousness preceding aposematism.
    - c) concluded that, at least for butterfly larvae, gregariousness is not explained as the pre-requisite to the evolution of aposematism via kin selection
  - ii. In a series of experiments with domestic chicks and aposematic/cryptically colored bug larvae, tested the hypothesis that gregariousness increases signal effectiveness of warning coloration:

a) falsified one alternative hypothesis : group size alone deters predation
    1) p/t: chicks should always attack solitary individuals more frequently than groups, even when groups are of palatable prey: clearly not met! (see figure)
    2) when chicks presented with groups of mealworms, attacked groups more frequently than solitaries – so group size alone doesn't decrease predation rate



b) direct test of hypothesis :
    1) predict that the proportion of naive birds attacking larvae will decrease with group size
    2) predict that the proportion attacking fourth instar (larger) larvae will less than the proportion attacking third instar (smaller) larvae across all group sizes: predictions clearly met



c) to falsify another alternative hypothesis for this particular predator: predict no significant decrease in attack rate in birds with prior experience (i.e., the opportunity to learn avoidance): statistical comparison showed no significant increase in learning with group size or size of individual prey items

d) conclusion: for chicks, at least, the size of the group magnifies the signal effectiveness of aposematic coloration

e) got same result with aversion and learning in experiments with great tits and seed bugs

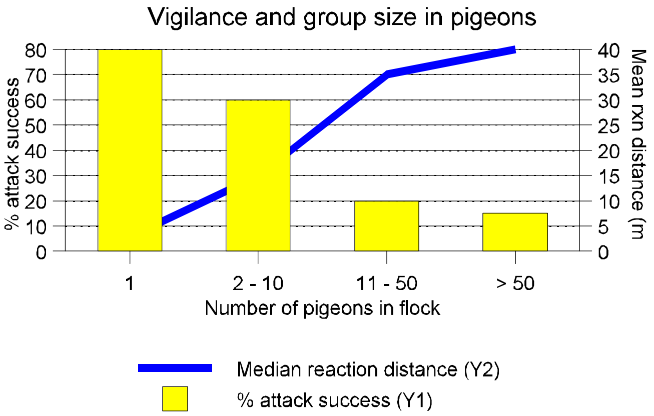
iii. for some species, however, experimental evidence does support increased learning with group size – so that's still a possibility for some species

7. Presence of aposematic colors/behaviors gives rise to **mimicry**, which can take two forms:
   - a. **Batesian mimicry**
     - i. def: palatable prey species (mimic) mimics noxious prey species (model)
     - ii. can only work when density of model species > density of mimic (think about why)
     - iii. common examples = flies, moths mimicking bees, wasps
     - iv. neat example = tephritid fly & jumping spider (see pic p. 17)
       - a) Family Tephritidae = "true fruit flies"
       - b) Within family have a variety of banding patterns on wings
       - c) For one species, banding pattern resembles spider legs; fly waves wings in pattern that seems to mimic predatory jumping spider defending its territory
       - d) experimenters tested mimicry hypothesis by performing wing transplants between tephritid flies and house flies:
         - 1) tephritids w/housefly wings behaved normally, but almost totally unable to "convince" jumping spiders to "back off"
         - 2) control flies (own wings removed and put back in place) escaped in 16 of 20 encounters

        3) houseflies with tephritid wings behaved normally and were also unable to avoid attack
      e) conclusion = both pattern and behavior are part of the mimicry system
      f) (think about how this kind of system might have evolved – i.e., the historical sequence)
      g) Read section on acoustical mimicry in burrowing owls, including experimental tests/evidence on your own.
      h) Another possible behavioral mimicry = colubrid snakes and rattlesnakes: colubrids spread backs of jaws, vibrate tails and hiss
  b. **Mullerian mimicry**
    i. def = multiple noxious species mimic each other (converge on same aposematic pattern)
    ii. examples include Monarch/Viceroy butterflies
  c. can get groups of species involving both kinds of mimicry – e.g. blennies:
    i. one species venomous (model)
    ii. one species not venomous, but has very sharp teeth that it uses for protection (Mullerian mimic of model)
    iii. one species completely palatable (Batesian mimic of both of the above)
8. Other adaptations for reducing attack rate (read examples on your own):
  a. associating with protective species
  b. advertizing unprofitability to pursue – e.g., stotting in Thompson’s gazelles: which predictions met?

Predictions	**Alternative hypotheses**			
	Alarm signal	Social cohesion	Confusion effect	Signal unprofitability
Solitary gazelle stots	no	yes	no	yes
Grouped gazelles stot	yes	no	yes	no
Rump directed to predator	no	no	yes	yes
Rum directed to gazelles	yes	yes	no	no

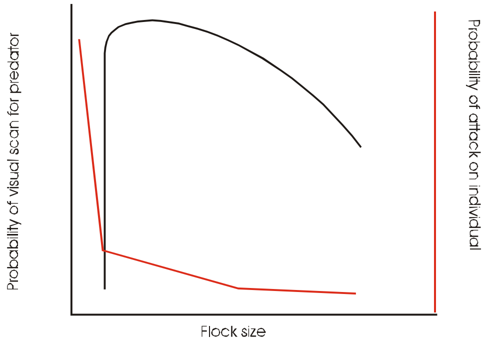
F. Making capture less likely
  1. Vigilance and sociality can reduce the likelihood of capture via several different mechanisms (not mutually exclusive):
    a. “many eyes”:
      i. hypotheses = as more individuals are watching predators
        a) likelihood of spotting one goes up
        b) response time decreases
        c) capture rate decreases
      ii. experimental and observational evidence:
        a) in many species, the larger the group the less time any one individual spends looking for predators (see table 4, e.g.)
        b) for caged starlings exposed to simulated predator, increasing group size decreased mean takeoff time after hawk released
        c) for wood pigeons exposed to live predators, increasing flock size increased median takeoff distance (distance of predator from flock)
        d) for wood pigeons, increasing group size decreased attack success of goshawk:



b. "selfish herd": aggregating with other individuals reduces each one's chance of being "the one" taken by predator
  i. key predictions from this hypothesis are that
    a) individuals should compete for access to safest positions within the herd
    b) even individuals in "least safe" positions within the herd are safer than are solitary individuals
  ii. e.g., bluegill sunfish
    a) breed in colonies, with males competing for central territories, which are preferred by females
    b) predation risk increases with distance from center of colony
    c) solitary nesters experience higher infestations of snails and spend more time chasing predators than do even individuals on edges of breeding colonies

c. "dilution effect": similar to "selfish herd", but simpler: large groups overwhelm consumption capacity of predators
  i. difference = in selfish herds, position within the herd influences risk of consumption; in "dilution" position is less important than total number

  - ii. e.g., redshank sandpipers form groups of over 30 birds:
    - a) don't get increased vigilance – in fact, as group size increases, the probability that any one individual is scanning for a predator decreases (opposite of "many eyes" hypothesis)
    - b) However, as group size increases, the probability of any one individual being attacked decreases



  - iii. this hypothesis may also explain masting in trees, synchronized emergence in insects (mayflies, cicadas)
- d. Other mechanisms that may reduce capture rates in social species are
  - i. use of alarm signals
  - ii. communal defense
  - iii. visual confusion (e.g., schooling fish, running zebras)

2. Other behaviors that can reduce capture rates (read examples – don't worry about data/evidence) are
   - a. "startle" responses
   - b. evasive action

G. Several mechanisms may be used to reduce the likelihood that an individual will be consumed even if it's captured (read examples on your own):

1. Chemical defenses and deterrents (intrinsic or "borrowed" from other species)

2. Misdirection (false heads, eyespots; autotomous tails, etc.)
3. Attracting other predators

H. Of course, these mechanisms aren’t mutually exclusive – read the section on Monarch butterflies and list all the mechanisms they use.