Montogue

Quiz BI109

Animal Behavior

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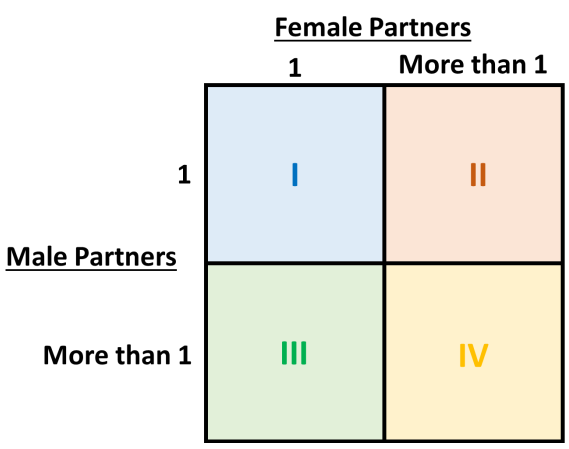
PROBLEMS

Conversation Starter

Animal mating systems are defined by the number of mates each sex has. The following schematic represents animal mating systems as functions of the number of mates of each sex. Choose the alternative that defines I to IV.



A) I. Polygynandry and promiscuity; II. Polygyny; III. Polyandry; IV. Monogamy
B) I. Polyandry; II. Monogamy; III. Polygyny; IV. Polygynandry and promiscuity
C) I. Monogamy; II. Polyandry; III. Polygyny; IV. Polygynandry and promiscuity
D) I. Monogamy; II. Polygyny; III. Polyandry; IV. Polygynandry and promiscuity

Problem 2

One aspect of mating behavior in some species is so-called *mate guarding*, in which a male individual prevents a female from mating with other individuals, thereby ensuring that the female will indeed bear the male's spawn and not those of another candidate. Some researchers have come to question the evolutionary benefits of mate guarding, as the energy and resources spent by a male in shielding a sexual partner from other individuals could instead be used to court and secure a second female for greater reproductive success. Nevertheless, mate guarding is common in the animal kingdom and may assume extreme forms, one of which is described below:

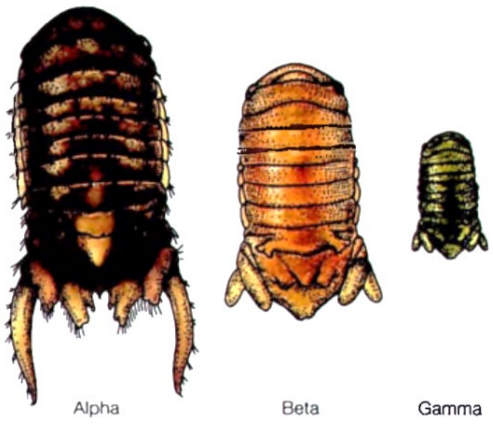
"*The most extreme commitments of this sort* [mate guarding] *occur when males sacrifice themselves after copulating, as happens, for example, when the male of the _____ expires after inserting both pedipalps (sperm-transferring appendages) into a female's paired genital openings. The dead male is then carried about by the female as a king of morbid chastity belt.*"

The extreme variant of "sacrificial" mate guarding described above occurs in:
A) The orb-weaving spider *Argiope aurantia*.
B) The solitary bee *Centris pallida*.
C) The black-winged damselfly *Calopteryx maculata*.
D) The common scorpionfly *Panorpa communis*.

▶ Problem 3

Regarding animal behavior theory, true or false?

The marine isopod *Paracerceis sculpta*, which resides in sponges found in the intertidal zone of the Gulf of California, is an example of species in which sexual selection has led to the development of very different body forms in the male sex (sexual dimorphism), as illustrated to the side. As shown, a male *P. sculpta* occurs in three sizes: *alpha*, *beta*, and *gamma*.



1.( ) Because mating behavior phenotypes are identical for the three types and the alpha type is physically stronger than the smaller betas and gammas, these latter two variants stand no chance to achieve reproductive success when scarcity of females places them in intraspecific sexual competition with an alpha. Alternative mating strategies have not evolved among betas and gammas to grant them access to a female when an alpha male is in the vicinities. ■ **(A black square indicates the end of a multi-paragraph statement.)**

Some species exhibit sexual conflict, that is, inharmonic reproductive behavior in which the two sexes battle for maximum genetic advantage. These behaviors may come in the form of coercion, as when a male takes advantage of its greater size and strength to force an unwilling female to mate, or may take the form of more subtle, elaborate mechanisms, most of which favor males, although some mechanisms have developed to favor the female sex.

2.( ) One example occurs in the mating dynamics of *Drosophila melanogaster*. When male flies of this species copulate with a female, the female takes advantage of the contact between reproductive systems to transfer a small amount of fluid enriched with a protein, Acp26F, that quickly gains access to the partner's system. After copulation ceases, the protein gradually elicits a host of negative effects in the male partner, including a disruption of sleep patterns, a lowered fecundity, and ultimately a shorter lifespan. ■

In an influential theory on the interface of mate selection and immunocompetence, Hamilton and Zuk proposed that at least some sexually selected traits are indicators of one ubiquitous environmental stressor: parasites. The focus on parasites followed from an earlier proposal that sexual reproduction evolved in the first place as a way to cope with parasites; specifically, by creating variability in the immune system that then provides more defenses against local parasites.

Infestation with parasites will lead to an increase in immune system activity that can suppress the secretion of testosterone. The decline in testosterone will result in poorly developed secondary sexual characteristics, which will then signal parasite infestation to would-be mates and competitors. Immunosuppression is predicted to be more evident in males in generally poor health than in males in better physical condition.

3.( ) The relation between testosterone, the expression of sexually selected traits and disease resistance is, however, nuanced and can vary across species, traits, and different features of the immune system. Across species, the relation between parasite load and testosterone is small, suggesting that high testosterone levels do not necessarily compromise immune functions. ■

Animal communication does not usually take place in isolation, but rather within a broader social context of third-party 'bystanders', and the importance of such individuals within a broader animal communication network has only quite recently received due attention.

It is known that among non-human primate infants, crying represents the principal form of vocal communication. Crying is particularly characteristic of interactions involving conflict between mother and offspring, such as when infants are rebuffed in their attempts to gain access to the nipple. The function of such crying is not well understood, but it is known that crying is likely perceptually noxious for other neighboring animals. The highly aversive nature of infant crying may, in

consequence, lead bystanders to be aggressive to the mother or the infant, in order to bring the crying bout to a close.
4.( ) Semple *et al.* (2009) put this hypothesis to the test by observing a free-ranging population of rhesus macaques (*Macaca mulatta*) in Puerto Rico. Importantly, those workers found little relationship between the presence of bystanders and potential aggression on their part towards mother and offspring. Furthermore, the presence of bystanders when the offspring was crying was found to produce no effect on the mother-offspring dynamic. ■

Recommended research: Semple, Gerald and Suggs (2009).

5.( ) Studies on the development of social intelligence in animal groups are lacking, especially in the case of long-lived vertebrate species. One notable exception is the paper of McComb *et al.* (2001), who tested vocal discrimination abilities in elephant populations in Kenya over the course of seven years. African elephants live in complex fission-fusion societies comprising different matrilineal family units led by the oldest female. Importantly, McComb and his collaborators found that societies led by younger females, which possessed better memory and vocal discrimination skills than older matriarchs, enjoyed greater reproductive success (as measured by the number of calves produced by the family per female reproductive year over the course of the study).

Recommended research: McComb *et al.* (2001).

6.( ) Apart from striking observations of tool use and manufacture, there are also important examples of complex cognitive abilities in birds. One of the most remarkable case studies on bird intelligence stems from Pepperberg's (Pepperberg, 2002; Pepperberg and Gordon, 2005) work with Alex, an African grey parrot (*Psittacus erithacus*). Alex was taught to name objects, identify the quality (i.e., size, shape or color) that a group of diverse objects have in common, and count from one to six. Furthermore, Pepperberg and her collaborators trained Alex to test the hypothesis that a nonhuman can represent the cardinality of a set by the numeral whose ordinal position in a count list determines its cardinal value; however, as reported in a 2012 paper (Pepperberg and Carey, 2012), that worker failed to show the development of number cardinality classification in a nonhuman species – even a cognitively superior bird such as Alex.

Recommended research: Pepperberg (2002); Pepperberg and Gordon (2005); Pepperberg and Carey (2012).

7.( ) Toolmaking among non-primate species is rare, but has been observed among some species. One fascinating example is Goffin's cockatoo, a medium-sized parrot endemic to the Tanimbar Islands, Indonesia. Like all parrots, they lack food caching or nest building ancestry, but nonetheless exhibit a strong, playful urge to combine objects. In a laboratory setting, Goffins exhibit sophisticated tool use and even tool manufacture. There is a so-called 'captivity bias' in toolmaking behavior among Goffin's cockatoos, in that it has rarely been observed in the wild; still, there are also recorded observations of tool use and toolmaking in these birds' native environment.

Recommended research: O'Hara *et al.* (2021).

One paper of importance in the quantitative study of animal communication is McCowan, Hanser and Doyle's 'Quantitative tools for comparing animal communication systems,' published in the journal *Animal Behavior* in 1999. The methods developed in the paper are underpinned by Shannon's information theory, which is independent of the kind of communication system of interest and thus enables a comparative examination of the complexity of vocal repertoires and their organization, both with respect to human language and, more generally, to behavioral ecology and evolutionary theory.
8.( ) Importantly, in the paper in question McCowan and her collaborators demonstrated the applicability of their model by applying it to the communication patterns of the North Atlantic pilot whale, *Globicephala melaena*. ■

Recommended research: McCowan, Hanser and Doyle (1999).

Recently, foraging models have begun to incorporate the notion of sensibility to risk. One aspect of such models is that foraging behavior is also dependent upon the amount of food offered in a patch and, most importantly, upon the variability of such nutrient supplies. With respect to such variability, the theory goes, a forager may be *risk averse*, avoiding patches with highly variable nutrient supply and instead going for the patches with least variance, or *risk prone*, opting for the patches with greater variance.
9.( ) As of yet, risk sensitivity in foraging is a purely mathematical concept and has yet to be demonstrated in experimental settings, be it involving carnivorous or herbivorous behavior. ■

Recommended research: Caraco, Martindale and Whittam (1980).

10.( ) Some species of insect have developed visual systems that enhance perception of certain colors and thereby improve their foraging behavior. To quote one example, some insect herbivores perceive color by a chromatic opponency system that compares the output from pairs of different cone classes. This mechanism is used by some aphids as a 'greenness' detector, that is, a system that responds to stimuli in such a manner that the closer the wavelength of incoming light is to green (the color often associated with leaves), the more intense the chromatic perception will be. Indeed, working with the mango hopper *Idioscopus clypealis*, Prokopy and Owens (1983) showed that this species of aphid is attracted to green objects but eschews the colors pink, purple, and yellow.

Recommended research: Prokopy and Owens (1983).

11.( ) One of the simplest forms of antipredator behavior is fleeing, that is, physically escaping from the grasp of a potential predator. Working with a variety of species, animal behaviorists have measured the so-called *flight initiation distance* (FID), or how close a predator can come before a potential prey will move away from it. Importantly, most studies indicate that the FID for a behavioral decision to flee to be taken is largely flexible for a given species, varying with factors such as the prey's closeness to a site of refuge (e.g., a coral reef close to a fish under threat) or the prey's prior experience with the same predator.

12.( ) Tonic immobility, also known as death-feigning behavior or thanatosis, is an antipredator behavior observed in various animal taxa including mammals, reptiles, amphibians, mites, and insects. In the red flour beetle, *Tribolium castaneum*, a genetic correlation between tonic immobility and activity levels has been observed. Furthermore, several studies have suggested a link between tonic immobility and the serotonergic system. It has been shown that the duration of tonic immobility in *T. castaneum* decreases with the administration of serotonin.

Recommended research: Nakayama *et al.* (2012).

13.( ) In lieu of death-feigning, some species of prey preserve themselves by diverting the attention of predators, either away from the prey or its young, or away from vital or vulnerable areas such as the head. Sometimes diversion is achieved by attention-grabbing movements, such as the tail-twitching displays of many lizards and snakes. Some lizards are able to break off the tail should an attack be carried through. The detached tail then squirms with a life of its own, keeping the predator occupied while the rest of the lizard makes its escape. The deliberate severing of a lizard's own tail is an example of *aposematism*.

14.( ) Societies of wild canids are some of the most well-documented in nature. Starting with anecdotal evidence gathered in the 1980s, researchers have indicated that there is prevalent interspecific hostility between canids, with important ecological and behavioral implications; Hersteinsson and Macdonald (1982, 1990) pioneered this line of research by showing that interspecific competition between the red fox and the arctic fox affects the geographic range of these species in regions where they are sympatric.

Recommended research: Hersteinsson and Macdonald (1982, 1990).

Modeling group hunting of African lions, *Panthera leo*, Scheel and Packer (1991) classified adhesion to group hunting in three types of strategy, namely *refraining* (non-participation in hunts), *conforming* (active participation in groups in which all individuals behaved similarly), and *pursuing* (active participation in groups where individual behavior varies). Those workers attempted to analyze group hunting dynamics in African lion groups by applying the game-theoretic approach that Packer and Ruttan (1988) had proposed some years earlier.

For species that capture single, large prey, Packer and Ruttan's models make four important predictions. First, the tendency to participate in prey capture is expected to increase with the difficulty of capturing a particular prey species. If the success rate of a lone hunter is very high, the participation of additional hunters can only improve capture rate slightly and thus the benefits of joining a hunt will be small relative to the costs. However, when success of a solitary hunter is very low, an additional hunter may improve the chances of capturing the prey sufficiently to overcome its own costs of participation. Second, poor hunters are expected to be less likely to participate than their more proficient companions, as the participation of an inept hunter will often have an insufficient effect on the success rate of the group to overcome its own costs of participation. Third, participation is expected to decline as the size of the hunting group increases; group hunting success increases asymptotically with increasing group size, and thus each additional animal's effort makes a smaller contribution to the success of the hunt. Fourth, the genetic relationship of the hunting group members is expected to influence participation; it is a general feature of models of cooperation that greater kinship among group members leads to group cooperation.

15.( ) In their investigation, Scheel and Packer found that age, group size, and kinship have substantial effects on the distribution of the three hunting strategies. On the other hand, hunting behavior was unaffected by sex – indeed, males and females under similar circumstances were equally likely to engage in refraining, conforming, and pursuing strategic behavior. ■

Recommended research: Scheel and Packer (1991); Packer and Ruttan (1988).

16.( ) Echolocation in animals that display such behavior works best when the loud outgoing vocalizations do not mask or reduce the listener's sensitivity to the weaker returning echoes. Most echolocators avoid forward masking effects by separating pulse and echo in time; however, about 160 species of bats in the families Rhinolophidae and Hipposideridae and the mormoopid *Pteronotus parnelli* separate pulse and echo information in frequency. A calling strategy based on separation of pulse and echo in time is known as *high duty cycle* (HDC) echolocation, while a strategy based on separation of pulse and echo in frequency is known as *low duty cycle* (LDC) echolocation.

Recommended research: Fenton, Faure and Ratcliffe (2012).

Due to environmental fluctuations, many species of temperate teleost fish face times when food supply is irregular, and many species have adapted to withstand long periods of starvation. Studies have shown that a wide variety of fish species experiencing food restriction often exhibit a compensatory growth spurt when food is made available.

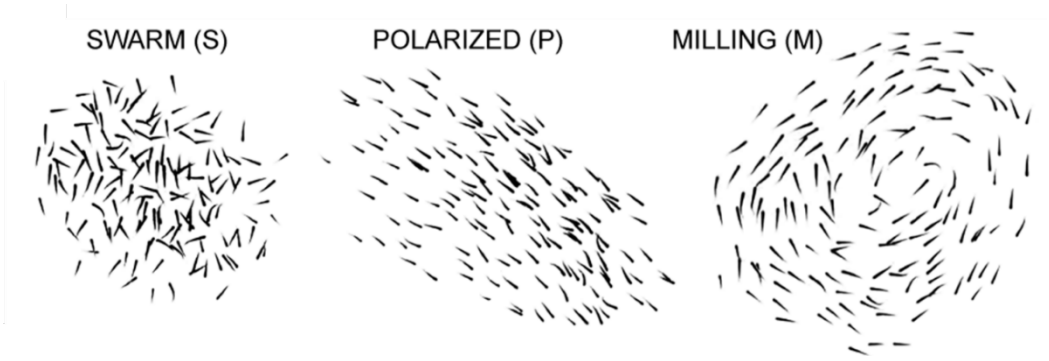
17.( ) One example of fish that display a hyperphagic response after wintering is the juvenile Atlantic salmon. Bull and Metcalfe (1997) investigated two specific aspects of the hyperphagic response of this species of salmon – feeding intensity and the duration of the appetite elevation – by submitting a group of fish to starvation for a time, then exposing them to a food supply, and ultimately comparing their response to that of a control group. The starved fish were divided into a group of 'very hungry' fish (i.e., fish that were starved for 40 days), 'hungry fish' (i.e., fish that were starved for 20 days), and controls. As expected, after they were exposed to a food source hungry or very hungry fish ate more than the controls. The two starved groups, 'hungry' and 'very hungry' fish, exhibited similarly high levels of hyperphagia for the duration of the experiment; importantly, after regaining access to food, the two starved groups also displayed hyperphagic behavior for the same period of time. ■

Recommended research: Bull and Metcalfe (1997).

The spontaneous emergence of pattern formation is ubiquitous in nature. Schooling fish are one of the mostly widely studied macroscopic group patterns, and have been shown to exhibit at least three dynamically-stable collective states: swarm, milling, and polarized groups.

18.( ) Importantly, research has shown that these three macroscopic organizational states occur in fish schools (say, 5 – 50 fish) in remarkably discrete patterns, as a school exhibits a single such pattern and does not rapidly transition to another (say, from swarm to milling, or from milling to polarized) without being exposed to some stressor, usually an external one (e.g., a rapidly approaching predator). A rapid alternation between two of the three school "states" under normal conditions is impossible. Furthermore, the size of the group (as measured in number of individuals) has no bearing on which structure is the most stable. ■

Recommended research: Tundstrøm *et al.* (2013).



19.( ) Assessing the diving behavior of black guillemot (*Cepphus grylle*), a circumpolar diving bird, Masden *et al.* (2013) found that the diving depth of this species decidedly does not coincide with the depth associated with tidal energy turbines and their movable parts. As a result, those workers suggested that consideration of black guillemot diving behavior be disregarded in the environmental impact assessment of marine energy projects.

Recommended research: Masden, Foster and Jackson (2013).

One important experiment on the interface between hormones, stress, spatial memory and behavior was conducted by de Quervain and his colleagues in the late 1990s. Those workers used a water maze to examine how one glucocorticoid hormone – corticosterone – affects spatial memory and habitat choice in rats. In their experimental setup, rats were put into a large tank of dark and murky water. Some distance from where the rat enters the water, there was a single small platform that was slightly submerged but close enough to the surface to serve as a resting place for the rat. The platform served as a refuge for the otherwise inhospitable habitat of the water tank. When first put into the tank, rats swim around randomly, but eventually come across the hidden platform and use it as a refuge.

On the basis of prior work on rodents, de Quervain and his colleagues hypothesized that a stress-induced increase in corticosterone would impair a rat's spatial memory regarding the position of the platform in their habitat. To test this hypothesis, they gave rats eight trials in the water maze, and then they divided the rats into four groups. In group I, rats received a shock 30 minutes before their ninth trial in the water maze. In group II, the shock was administered two minutes before the ninth trial. In group III it was administered four hours before the ninth trial. A fourth group – the control group – received no shock before their ninth trial. De Quervain and his team found that rats in groups II and III spent about as much time near the platform as did rats in the control group. That is, shocks that were administered two minutes or four hours before a trial did not impede spatial memory for the location of the platform. Rats in group I – those that experienced the shock 30 minutes before the trial – did show impaired memory for the location of the platform.

20.( ) De Quervain and his colleagues then measured corticosterone levels in all four groups. Importantly, they found higher levels of corticosterone in rats of group I, but not in rats of groups II, III, and IV; those workers thus established a spatial memory-inhibiting role for corticosterone, albeit one associated with median duration only, as rats exposed to the maze just before (group I) or a long time before (group III) being stressed still reached the platform with ease. ■

Recommended research: Masden, Foster and Jackson (2013).

Division of labor, social roles and reproductive skew are exemplified most clearly in the highly structured societies of eusocial species. *Eusociality* is characterized by division of labor based on a caste system, in which some members of the group lose their ability reproduce altogether and become a sterile 'worker' class on behalf of other, reproductive, individuals (often referred to as 'kings' and 'queens'). Other key features of eusoicial systems are cooperation in care of young, and the maintenance of at least two overlapping generations capable of sharing the group labor, although these features are also displayed by some non-eusocial species, such as birds.
21.( ) The most well-documented cases of eusocial behavior occur in insects, especially hymenopterans (ants, bees and wasps) and termites. However, eusociality has also been observed in aphids and beetles. ■

22.( ) A honeybee that has just returned from foraging can communicate information about its findings by dint of the so-called *waggle dance*. Depending on the bee's movements, the bee can inform of its sisters about the direction of a potential food source, including its position relatively to the hive and the sun. Even the duration of the dance affords information: The longer the waggle dance, the farther away the bounty is.

Like the honey bee, another species that exhibits remarkable spatial memory is Clark's nutcracker, a crow-like bird that lives in the high coniferous forests of the western North American mountains. In these regions, there is a marked seasonal pattern of availability of pine seeds, and by late autumn or early winter virtually no seeds remain on the trees or on the surface of the ground. Yet Clark's nutcrackers that live all year round at these elevations depend on these seeds for food throughout the winter and spring, including the breeding season. To prepare for periods of food scarcity, the nutcracker hides tens of thousands of seeds in several thousand separate caches in the soil, mostly on south-facing slopes. This behavior indicates that nutcrackers can remember the location of their caches for many months.
23.( ) Balda and Kamil (1992) put nutcrackers to the test and found that they exhibited superior ability to recall the location of seed caches even 285 days after storing food in them. Importantly, those workers verified that the presence of landmarks and other spatial cues had no effect on the recalling performance of the nutcrackers. Also worth mentioning is those workers' finding that odor cues from seeds played a crucial role in the birds' ability to recover cache locations. ■

Recommended research: Balda and Kamil (1992).

24.( ) Like bees, leaf-cutter ants often forage in groups and hence must communicate with precision their findings to fellow ants. The main mechanism of communication in such ants is stridulatory vibrations; use of semiochemicals such as pheromones has no role in their intraspecific foraging behavior, at least not in species of the *Atta* genus.

▶ Problem 4

Most birds capable of communicate via *birdsong*, as it is commonly defined, belong to the suborder Passeri and are known as Oscines. For scientific purposes, Oscine songs are often divided into ever smaller groups of sounds. Which of the following alternatives contains the traditional hierarchy of birdsong sounds in order of increasing duration?
A) Syllable → Element → Phrase → Song
B) Element → Syllable → Phrase → Song
C) Syllable → Phrase → Element → Song
D) Element → Phrase → Syllable → Song

▶ Problem 5

Building behavior is observed among invertebrates such as termites, spiders and bees, but it is in avian nests that we find some of the most structurally complex examples of building activity known to man. According to Hansell (2000), the composition of a bird's nest consists of four functionally distinct areas. Which of the following alternatives correctly ranks the four nest zones from outermost to innermost?
A) Outer (decorative) layer → Attachment → Structural layer → Lining
B) Outer (decorative) layer → Attachment → Lining → Structural layer
C) Attachment → Outer (decorative) layer → Structural layer → Lining
D) Attachment → Structural layer → Outer (decorative) layer → Lining

▶ Problem 6

Birds navigate by day and night, and use celestial cues to enable them to do so. By day the sun is the dominant cue and at night it is replaced by the stars. Of course, the sun is not a stationary body. The azimuth moves during the course of the day and so birds using it for navigation must use a bi-coordinate system that takes account of both solar position and time. Clock-shifted starlings, i.e., birds that have been conditioned in captivity to be out of sync with natural daytime, have been used in experiments to demonstrate this. If a starling is conditioned to be positively clock-shifted by 6 hours, so that a bird perceives the time of day to be 6 hours later than it actually is, a starling released at 6 AM will, most likely (assume the azimuth of the sun changes 15° per hour):

A) Fly in an orientation displaced 15 degrees relatively to the orientation of a "normal" starling flying at 6 AM. The clock-shifted starling would fly as it would at 12 AM.

B) Fly in an orientation displaced 90 degrees relatively to the orientation of a "normal" starling flying at 6 AM. The clock-shifted starling would fly as it would at 12 AM.

C) Fly in an orientation displaced 15 degrees relatively to the orientation of a "normal" starling flying at 6 AM. The clock-shifted starling would fly as it would if it were noon.

D) Fly in an orientation displaced 90 degrees relatively to the orientation of a "normal" starling flying at 6 AM. The clock-shifted starling would fly as it would if it were noon.

SOLUTIONS

P.CS ➡ *Solution*

Monogamy occurs when mating patterns are characterized by crossings between one male and one female. *Polygyny* occurs when males have multiple partners but females have just one. *Polyandry* occurs when females have multiple partners but males have just one. *Polygynandry* occurs when both males and females of some species mate with multiple partners, and such matings involve pair-bonds between the males and females. Lastly, *promiscuity* occurs when both males and females mate with multiple partners and matings are seemingly random, with no association between mates beyond sperm transfer.

- The correct answer is **B**.

P.2 ➡ *Solution*

The odd mating behavior in question occurs in the orb-weaving spider *Argiope aurantia*.

- The correct answer is **A**.

P.3 ➡ *Solution*

1. False. In actuality, isopods have developed behavioral polymorphism that may enable betas and gammas to achieve reproductive success even when threatened by their larger counterparts. As Rubenstein and Alcock (see reference below) report, gammas avoid alpha males as much as possible and may try to sneak matings with females living in their sponges. When an alpha and a medium-size beta male meet inside a sponge cavity, the beta behaves like a female, and the male courts his rival ineffectually. Through female mimicry, the female-size beta males coexist with their much larger and stronger rivals and thereby gain access to the real females that the alpha males would otherwise monopolize.

Reference: Rubenstein and Alcock (2018).

2. False. Actually, things work a little differently. The protein Acp26F is transferred from the male to the female, not the opposite, and works to boost male reproductive success (perhaps by damaging rival sperm) at the expense of the female, shortening the female's life, disrupting its sleep patterns, and lowering its fecundity. Despite the negative long-term effects that toxic protein donors have on their mates, males still gain because they are unlikely to mate with the same female twice. Under these circumstances, a male that fertilizes a larger proportion of one female's current clutch of eggs can derive fitness benefits even though his chemical donations reduce the lifetime reproductive success of his partner.

3. True. Indeed, Geary (see reference below) notes that across species the relation between parasite load and testosterone is small, suggesting that high testosterone levels do not necessarily compromise immune functions. Nevertheless, Geary notes that these observations do not invalidate the immunosuppression model entirely when, in fact, the prediction is that males in good health can tolerate both high testosterone levels – leading to full expression of sexually selected traits – and high parasite loads. It is males that are in marginal health that will pay the immunity price of trait expression.

Reference: Geary (2015)

4. False. In actuality, Semple and his group found that crying was associated with increased aggression from bystanders towards mothers and infants, especially in the case of 'high-risk' bystanders (i.e., bystanders that posed a high risk of aggression to the mother). Furthermore, the presence of bystanders influenced the mother-offspring dynamic, in that mothers were less likely to yield access to nipples when no bystanders were present compared to situations when low-risk or at least one high-risk bystander were present.

Reference: Semple *et al.* (2009).

5. False. Much to the contrary, McComb *et al.* (see reference below) verified that it was older matriarchs, not younger individuals, that exhibited superior social discrimination skills. The superior discriminatory abilities of older matriarchs should translate into reproductive benefits for the family unit, because time is more efficiently allocated by reserving defensive behavior for circumstances where it is appropriate, and because opportunities for cooperation with more frequent associates are provided.

Reference: McComb *et al.* (2001).

6. False. Pepperberg and Carey (see reference below) showed that Alex was actually able to rank the Arabic numerals 6, 7 and 8. What's more, with no further training he was able to integrate the ordinality of these numerals with those he already knew (1 – 6).

Reference: Pepperberg and Carey (2012).

7. True. The study quoted in the statement (O'Hara *et al.*, see reference below) reports the occurrence of tool manufacture and use to extract seed matter of a tropical fruit in two wild Goffins. O'Hara and his team concede that such behavior is still an exception, not the rule; prior to the publication of their work, nearly 890 hours of observational footage in the native environment of Goffins had failed to indicate any instance of tool use and manufacture.

Reference: O'Hara *et al.* (2021).

8. False. Actually, McCowan's team worked illustrated their model with an application to the bottlenose dolphin (*Tursiops truncatus*).

Reference: McCowan, Hanser and Doyle (1999).

9. False. Actually, experimental studies on risk-sensible foraging date have been published for several decades. One early example is that of Caraco, Martindale and Whittam (see reference below), who, working with yellow-eyed juncos, presented birds with two trays containing birdseed, such that once a bird made the choice to go to one tray, the other was immediately removed. One tray had a "fixed" amount of food – for example, a fixed tray might always have five seeds – while the other tray had a "variable" amount of food – for example, no seeds half the time, and ten seeds half the time. The variable tray had a mean number of seeds (five) equal to that on the fixed tray. Caraco was able to show that birds on a negative energy budget (i.e., underfed ones) valued additional food items more than those on a positive energy budget. Risk-sensitive theory predicts that birds on a positive energy budget should choose the fixed trays, while very hungry birds should choose the variable trays. The juncos in Caraco's study behaved in a fashion very similar to that predicted from theory, that is, birds on a positive energy budget mostly chose the fixed trays, while very hungry birds often chose the variable trays.

Reference: Caraco, Martindale and Whittam (1980).

10. False. Interestingly, Prokopy and Owens (see reference below) reported that *I. clypealis* was more driven to yellow sticky traps (devices hung vertically with the branch/twig under the canopy of mango trees) than to sticky traps of different color, including green ones. In ecological terms, one possible explanation for this is that the mango trees that this aphid preys upon exhibit

yellow leaves during senescence. Hence yellow has been referred to as a 'super-normal foliage-type stimulus.'

Reference: Prokopy and Owens (1983); excerpt from Ryan and Wilczynski (2011)

11. True. FID is in fact quite affected by a number of factors within the same species. Researchers have noted that animals that were far from a refuge (their territory, for example) initiated fleeing from a predator sooner than animals closer to their refuge. Likewise, it has been found that prey typically flee at a greater distance as a function of their experience with predators. Other factors also influence the behavioral decision of when to flee including the presence or absence of some kind of armoring on part of the prey, and potential tradeoffs between fleeing and simultaneous behaviors, such as foraging.

Reference: Dugatkin (2014).

12. False. The statement would've been correct had the references to serotonin and the serotonergic system been replaced with references to dopamine and the dopaminergic system. The duration of thanatosis in *T. castaneum* decreases with the administration of dopamine, and there is a negative relationship between brain dopamine levels and the intensity of tonic immobility. Nakayama *et al.* (see reference below) note that the duration of tonic immobility decreases with the administration of caffeine, which is known to increase the activity of dopamine receptors.

Reference: Nakayama *et al.* (2012).

13. False. A deliberate severing of a lizard's own tail is actually an example of *autotomy*. Autotomy of body parts is also known in organisms such as annelids, molluscs, and arthropods, while tail-stripping (shedding the skin and flesh of the tail) may serve a similar function in some small rodents. As any student who has taken an introductory biology course may know, *aposematism* is an entirely different form of defense, in which the prey relies on the toxic, distasteful, or otherwise noxious qualities of the prey's own tissues.

Reference: Barnard (2004).

14. True. As noted by Hersteinsson and Macdonald (see references below), the behavior and biology of arctic and red foxes are quite similar, which makes interspecific competition a likely relevant factor in their geographic range wherever the two species occur sympatrically; indeed, those two workers quote a host of references indicating that decreases in arctic fox distribution and abundance occur concomitantly with red fox range expansions.

References: Hersteinsson and Macdonald (1982, 1990).

15. False. Some of the associations mentioned in the statement should've been swapped. Scheel and Packer (see reference below) note that while age and sex are both likely to correlate with hunting proficiency, only the latter was found to have appreciable effect on any measure of hunting participation. Indeed, males had a higher probability of refraining than females, and a lower probability of pursuing. In addition, a lower proportion of males present joined rushes.

Moreover, Scheel and Packer found that no measure of lion participation changed significantly with group size while hunting any of the four types of prey considered in the study. In addition, they found no effect of the average degree of maternal kinship on the probability that females pursued, refrained, or conformed in a group hunt, when kinship was estimated either for the whole pride or only for those individuals present at the hunt. However, those workers concede that the estimates of kinship they used were coarse, and that after controlling for prey species their sample size may have been too small to detect either group size or kinship effects.

Reference: Scheel and Packer (1991).

16. True. As mentioned in the statement, time-based pulse-echo separation is LDC echolocation, while frequency-based pulse-echo separation is HDC echolocation. In an interesting study, Fenton *et al.* (see reference below) explored the evolution of HDC echolocation in bats, noting that features associated with HDC echolocation – long duration calls dominated by a constant frequency (CF) component, an acoustic fovea, and Doppler shift compensation – allowed bats to detect, lock onto and track fluttering insects. It followed that HDC echolocation originated because it allowed hunting bats better access to nocturnal prey, especially in cluttered habitats.

Reference: Fenton, Faure and Ratcliffe (2012).

17. False. While it is true that both 'hungry' and 'very hungry' fish exhibited similarly intense bouts of hyperphagia after regaining access to food, the 'very hungry' fish actually maintained higher levels of feeding behavior for longer than the hungry fish. This suggests that starvation resulted in a strong motivation to feed in both groups, but that as a result of their higher energy deficit the very hungry fish were motivated to feed at higher levels for a longer period.

Reference: Bull and Metcalfe (1997); excerpt from Scott (2005).

18. False. The consensus gleaned from observation and simulation is that rapid structural transitions in school states are very much possible. Tracking schools of golden shiner (*Notemigonus crysoleucas*), Tunstrøm *et al.* (see reference below) showed that groups frequently transitioned between the three collective states. Also in contrast to what is said in the statement is those workers' finding that the size of the group in fact influenced which of the three formations was most stable; indeed, they found that for the smallest group size of 30 fish the polarized state predominated, whereas for groups of 150 to 300, individuals spent most of their time milling.

Reference: Tundstrøm *et al.* (2013).

19. False. Actually, Masden *et al.* (see reference below) reported that 62% of the dives recorded in their study were in water deep enough to accommodate a turbine (i.e., more than 30.5 m). Furthermore, 37% of diving time was spent between 8 and 26 meters, a depth range that may contain rotors. As a result, those workers concluded that black guillemots dive to depths at which tidal turbines are likely to operate and should therefore be considered thoroughly in environmental impact assessments and marine planning.

Reference: Masden, Foster and Jackson (2013).

20. True. Indeed, de Quervain *et al.* (see reference below) established a relation between exposure to a stressor – in this case, an electric shock – heightened levels of corticosterone, and spatial memory. Since increased hormonal levels were verified specifically in the rats that were shocked 30 minutes before entering a ninth trial, but not on those stressed just before or a long time before entering the maze, a memory-inhibiting effect for very short-term and longer-term intervals could not be established.

Reference: De Quervain, Roozendaal and McGaugh (1998); excerpt from Dugatkin (2014).

21. True. Indeed, eusocial behavior has been documented in some aphids and beetles. Until recently, eusociality was thought to be restricted to insects, but has since been observed in two species of mammal, the naked mole rat (*Heterocephalus glaber*) and Damaraland mole rat (*Cryptomys damarensis*), as well as a crustacean, the snapping shrimp (*Synalphaus regalis*).

22. True. Indeed, the longer the bee dances – in a part of the waggle dance known as the "straight line" – the farther away the bounty is from the hive.

23. False. The statement errs twice, first by mentioning that landmarks play no role in the nutcrackers' ability to locate the caches – Balda and Kamil (see reference below) quote studies indicating that they do – and second by indicating that odor cues are crucial to pinpointing the location of the caches – they are not.

References: Balda and Kamil (1992).

24. False. Some chemicals are in fact implicated in the foraging behavior of *Atta* ants, namely methyl 4-methypyrrole-2-carboxylate and 3-ethyl-2,5-methylpyrazine. These substances are produced in the poison gland of leaf-cutter ants and may be used to recruit workers to foraging sites located away from the nest.

Reference: Dugatkin (2014).

P.4 ➡ *Solution*

A typical chaffinch song, for example, consists of a number of distinct sections. These are called *phrases*, and each phrase consists of a series of units which occur together in a particular pattern. Sometimes, the units in a phrase are all different, and hence can be subdivided into smaller segments referred to

as *syllables*. Syllables can be very simple or quite complex in their structure. When complex, they are constructed from several of the smallest building blocks of all, called *elements* or *notes* (although the latter is usually avoided because of its musical connotations).

♦ The correct answer is **B**.

P.5 ➡ *Solution*

Alternative B correctly ranks the four bird nest zones. The most important of the four nest zones, Hansell (see reference below) notes, is the structural layer; the critical feature of this zone is that it gives integrity to the nest shape, preventing it from distorting or falling apart. Any component of the nest considered to be performing this role is treated as a component of the structural layer.

Reference: Hansell (2000).

♦ The correct answer is **C**.

P.6 ➡ *Solution*

A starling positively clock-shifted by 6 hours will fly at 6 AM as it would six hours later, at noon. Since the azimuth changes 15° per hour, the starling would fly at an orientation shifted $6 \times 15 = 90°$ relatively to the orientation of a "normal" starling flying at 6 AM.

♦ The correct answer is **B**.

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