SPECIAL ISSUE: COGNITIVE ECOLOGY

Animal Behaviour 147 (2019) 199–210

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Cognitive Ecology

Animal expertise: mechanisms, ecology and evolution

Reuven Dukas*

Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON, Canada

ARTICLE INFO

Article history:
Received 29 November 2017
Initial acceptance 5 March 2018
Final acceptance 4 May 2018
Available online 5 June 2018
MS. number: SI-17-00947

Keywords:
cognition
evolution
expertise
heritability
learning
life history

Expertise consists of the features that allow individuals with extensive experience on a given complex task to show superior performance on that task compared to novices. While expertise has been investigated mostly in humans, it is highly relevant for other species as well because it can have strong effects on fitness. Moreover, studying expertise in nonhumans can help us understand human expertise. Several features that distinguish experts within their domain of expertise from novices include (1) greater long-term memory, (2) larger capacity of working memory, (3) better ability to focus attention on the most relevant concurrent tasks, (4) superior ability to anticipate, perceive and comprehend the relevant elements in one's surroundings, (5) quicker and better decisions, and (6) faster and more coordinated motor movements. The development of expertise follows a characteristic pattern of gradual improvement in performance over extended periods devoted to practising a given complex task. Heritable variation in a few traits can affect the rate of expertise acquisition and its peak levels. These traits include motivation to practise, perseverance, basic cognitive abilities such as attention span, working memory capacity, learning rates and memory retention, and various physiological, anatomical and morphological features. Key environmental factors influencing expertise development are parental and social settings, which may encourage investment in the extended practice necessary for achieving superior performance on complex tasks. Future work on the evolutionary biology of expertise should focus on the yet unknown neurobiological mechanisms that underlie it, heritable variation in the traits that enable expertise and their genetic basis, further quantifications of expertise acquisition in natural settings, the fitness consequences of the traits that facilitate top expert performance, and the ecological and evolutionary consequences of expertise.

The historically dichotomous nature of the literatures on human and nonhuman cognition is gradually fading as researchers in multiple disciplines replace entrenched traditions with an appreciation of the fundamental similarity among all animals including humans (Dukas, 1998a; Richards, 1987). While old notions about the dominance of instincts in nonhuman animal behaviour (Fabre, Teixeira de Mattos, & Miall, 1918; Tinbergen, 1951) have given way to sophisticated understanding of the important roles of learning and other cognitive abilities (e.g. Dukas, 2009; Shettleworth, 2009), expertise research has been mostly restricted to humans (Ericsson & Lehmann, 1996; Ericsson, Charness, Feltovich, & Hoffman, 2006). Expertise may be defined as the characteristics, skills and knowledge allowing individuals with extensive experience to perform significantly better than novices on a given complex task (Dukas, 2017).

There are three substantial reasons for expanding expertise research to nonhuman species. First, while the human literature has identified unique mechanisms enabling expertise (e.g. Bor & Owen, 2007; Diedrichsen & Kornysheva, 2015; Wymbs, Bassett, Mucha, Porter, & Grafton, 2012), we still lack fundamental understanding of their evolutionary biology, genetics and neurobiology. Second, data consistent with the gradual development of expertise in the domains of foraging, survival and reproductive success exist for a variety of species including bees, birds and mammals (De Resende, Ottoni, & Fragaszy, 2008; Dukas, 2008a; Dukas & Visscher, 1994; Leach & Sedinger, 2016; Lonsdorf, 2005; Rutz, 2012; Wooler, Bradley, Skira, & Serventy, 1990). Finally, research on human expertise has focused on practice as the best predictor of top performance (Ericsson, Krampe, & Tesch-Römer, 1993; Ericsson & Pool, 2016). However, the contributions of extensive practice to performance remain understudied in all disciplines of animal biology including animal cognition and behaviour.

A broad, integrative biological framework that includes mechanisms, ecology and evolution can advance research on expertise. First, expertise can be positively associated with fitness and hence

* Correspondence: R. Dukas, Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada.
E-mail address: dukas@mcmaster.ca.

https://doi.org/10.1016/j.anbehav.2018.05.010
0003-3472/

influence the evolution of a variety of cognitive, behavioural and life history traits (Dukas, 2017). Second, an evolutionary biological approach and use of animal models can enhance our understanding of human expertise. Here I will (1) briefly review key findings from the vast literature on human expertise, (2) discuss a few examples of nonhuman species that show performance patterns resembling human expertise, (3) assess the mechanisms underlying expertise, (4) evaluate key traits that determine individual variation in performance and their association with expertise and (5) outline major future directions.

HUMAN EXPERTISE

To illustrate human expertise, I present two examples, one dealing with surgery, a modern, specialized skill performed by a small proportion of people, and the other with hunting, a universal skill practised in the past by most men. Surgeons go through extensive training, which includes 4 years of medical school, 5 years of residency, and often, an additional 3-year fellowship devoted to acquiring specific expertise within a narrow subdiscipline. In spite of this elaborate preparation, substantial data indicate that practicing surgeons become better with experience, as determined by objective measures of surgery success. A study of 72 surgeons who removed the prostates of 7765 prostate-cancer patients examined the association between surgeons' prostatectomy experience and surgery success, as measured by the standard criterion of no cancer recurrence within 5 years (Vickers et al., 2008). Because outcomes depend on the pathologic stage of the cancer, cases were divided into early stages, in which the cancer is confined to the prostate, and late stages, where cancer is spread into surrounding tissue. For both stages, there was a dramatic increase in surgery success with surgeon experience. With the early stages, success rate went from 85% for the least experienced surgeons to almost 100% for the most experienced surgeons, who performed over 1500 prostatectomies (Fig. 1a).

While the prostatectomy example did not provide a within-surgeon analysis of improvement with experience, there are ample anecdotal data indicating that such enhancement, which involves perfecting numerous subtle skills, is the rule (Birkmeyer et al., 2002; Bridgewater et al., 2004; Gawande, 2002). Notably, even expert surgeons show dramatic improvement when they have to adopt new, superior surgical techniques. Such transitions are often accomplished with minimal coaching. Instead, the surgeons attain the new expertise through trial and error at an initial cost to unlucky patients (Gawande, 2002). For example, when surgeons started treating newborns with a severe heart defect (transposition of the great arteries) using the 'switch' operation, mortality rates were close to 30%, compared to 6% with the standard 'senning' procedure. Quickly, however, infant mortality with the superior 'switch' operation declined, resulting in close to 50% increase in infant's expected life span with the new than with the old technique (Bull, Yates, Sarkar, Deanfield, & de Leval, 2000).

Unlike surgery, hunting among hunter–gatherers is a basic task that all men are expected to carry out. However, locating target animals and hunting them using traditional tools such as bows and arrows or spears is a very challenging undertaking. The hunter has to be proficient at identifying animals based on visual cues, smells, sounds, tracks and scats, knowing their habits and spatial and temporal availabilities, and interpreting tracks and other cues indicating relevant information including age, sex, body condition, activities and vulnerabilities (Liebenberg, Louw, & Elbroch, 2010). The hunter then has to stealthily approach his target from the optimal direction and route while considering wind direction and intervening vegetation. When shooting an arrow, the hunter again has to consider the intervening vegetation as well as wind speed and direction. He then

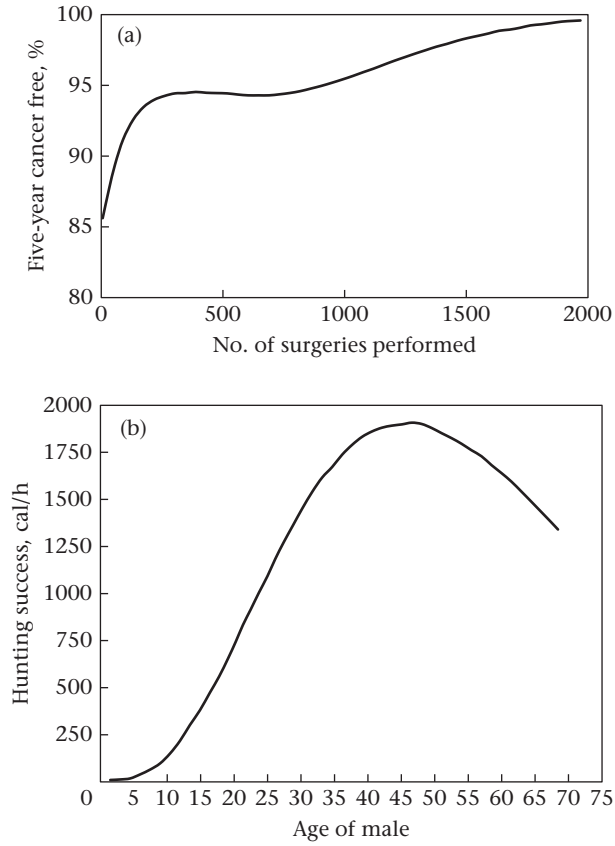

Figure 1. (a) Percentage of patients that were free of cancer 5 years after removal of a cancerous prostate gland as a function of their surgeon's experience. Data from Vickers et al. (2008). (b) Hunting success as a function of age in hunter–gatherer men from the Machiguenga and Piro of southeastern Peru. Data from Gurven and Kaplan (2006).

has to correctly calculate the arrow trajectory, which requires substantial experience with applying the proper force and angle (MacDonald, 2007; Walker, Hill, Kaplan, & McMillan, 2002). Finally, the construction of bows and arrows involves extensive technical knowledge, complex manufacturing skills and superb sensorimotor coordination (González-Ruibal, Hernando, & Politis, 2011). For example, early in the 20th century, Lothrop (1928) documented the painstaking process of bow and arrow construction among the hunter–gatherers of Tierra del Fuego. While only a few highly skilled artisans constructed the bows, most men made their own arrows. To make the arrows, they had to first collect six distinct materials from the beach, plains and mountains, and then use seven different tools during a 14-step manufacturing process.

Several studies of hunter–gatherers including the Gidra Papuans of lowland Papua New Guinea (Ohtsuka, 1989), the Ache of eastern Paraguay (Walker et al., 2002), the Machiguenga and Piro of southeastern Peru (Gurven & Kaplan, 2006), Tsimane of lowland Bolivia (Gurven, Kaplan, & Gutierrez, 2006) and the Hadza of northern Tanzania (Blurton Jones & Marlowe, 2002) quantified hunting success as a function of age. The common finding in all these studies is that men reach peak hunting performance between their mid-30s to upper 40s (Fig. 1b) and that the main factor explaining this relatively late-life peak is the gradual increase in hunting expertise.

Features of Expertise

The above examples of human expertise (Fig. 1) focused on performance as a function of experience as this is the defining

feature of expertise. What are, however, the general characteristics that distinguish experts from novices? While some aspects of expertise are unique to specific domains, one can readily list a core set of general features (Table 1). First, the knowledge base of experts is extensive and is often based on the acquisition of relevant information over decades. For example, human infants initiate a long process of learning a rich language that includes a vocabulary of 50 000–100 000 words by midlife (Clark, 2009).

Second, experts effectively have an expanded working memory because they can overcome the limited capacity of working memory by integrating it with long-term memory (Ericsson & Kintsch, 1995). Practically, this means that experts can handle a greater amount of information within their expertise at any given time than novices (see Mechanisms of Expertise below). For example, when chess players differing in skill levels were asked to scan a mid-game chess board for a few seconds and then reconstruct from memory the locations of all pieces, novices correctly recalled five pieces whereas experts recalled 20 pieces (Chase & Simon, 1973; Gobet & Simon, 1996).

Third, because experts can pay minimal attention to well practiced tasks, they can devote more attention to other, more attention-demanding aspects of a complex undertaking. For example, people initiating driving lessons in a manual transmission vehicle find it very challenging. In addition to the multiple tasks required of a driver in an automatic transmission car, manual transmission involves a long list of steps. For instance, shifting from fourth to fifth gear involves the following steps: release the gas pedal, press the clutch, shift gear lever forward, shift lever to right, shift lever forward, release the clutch, press the accelerator down. While this cumbersome series of coordinated hand and foot movements initially requires significant attention, expert drivers perform it as if it were an easy single step requiring negligible attention (Schmidt & Lee, 2011, page 450). Consequently, they can devote more attention to other information relevant for safe driving. Indeed when novice and expert drivers of automatic and manual transmission cars were asked to drive in a busy downtown and report all instances of 'children at play' road signs, there was a significant interaction between drivers' levels of expertise and transmission type. Novice drivers of manual transmission cars showed 13% lower sign detection rate than did novice drivers of automatic transmission cars compared to only 4% difference between the expert treatments (Shinar, Meir, & Ben-Shoham, 1998). In addition to having a reduced attentional load, experts rely on their experience to optimize their attentional allocation, with more attention devoted to either spatial locations or features with potentially greater effects on performance (Dukas, 2002; Shaw & Shaw, 1977).

Fourth, experts show superior situation awareness, defined as the anticipation, perception, comprehension and projection of all relevant elements in one's surroundings (Endsley, 2006). For example, an analysis of pilot performance identified key features distinguishing novices from experts. Novices showed monitoring deficiencies and difficulties in the required multitasking. They also had poorly developed mental models of all the necessary information required for flying and landing in new locations. Indeed an analysis of the Aviation Safety Reporting System database indicated that the largest single category of air-traffic incidents involved failure to monitor or observe available information (Endsley & Jones, 2004).

Fifth, the greater relevant knowledge in both long-term and working memory enables experts to execute faster and better decisions. For example, when novice and expert chess players competed under time constraint (5 min games), the experts maintained high performance levels while the novices made more poor moves compared to their games under standard duration (Calderwood, Klein, & Crandall, 1988).

Sixth, experts perform motor tasks with greater speed, precision and temporal and spatial coordination (Diedrichsen & Kornysheva, 2015; Schmidt & Lee, 2011). For example, professional pianists have higher maximum finger-tapping rates, greater spatial precision and higher timing accuracy than amateur pianists (Krampe, Engbert, & Kliegl, 2002; Telford & Spangler, 1935). Finally, it is worth emphasizing that expertise is always domain specific because it requires extensive training within that domain, which typically lasts a significant portion of one's lifetime. For example, we do not expect top chess players to perform above average in either a piano recital or in surgery.

Table 1
Major characteristics that distinguish experts within their domain of expertise from novices

Characteristics of experts
1. Greater long-term memory
2. Enhanced working memory
3. Better allocation of attention among co-occurring subtasks
4. Superior situation awareness, defined as the anticipation, perception, comprehension and projection of all relevant elements in one's surroundings
5. Quicker and better decisions
6. Faster, more precise and greater temporal and spatial coordination of motor movements

See the main text for details, examples and references.

Factors Other Than Experience

The extensive data on human expertise are compelling (Ericsson et al., 2006). Given the nature of expertise, however, the research often involves either a comparison between experts and matched nonexperts, or an assessment of groups that differ in either age or some measure of cumulative practice. That is, one cannot randomly assign human subjects to expert and nonexpert treatments and then record their performance over many years. Consequently, many expertise studies suffer from sample selection biases (Heckman, 1979). For example, starting with a random group of novices, the individuals not progressing well will be more likely to drop out. Hence, the apparent effects of extensive experience are positively correlated with other traits that influence individual performance and rate of improvement including motivation, effort, cognitive abilities, perseverance and anatomical, physiological or morphological features. The best way to address this issue is to conduct a proper experiment with an appropriate model species in which subjects are randomly assigned to expert and nonexpert treatments. Additionally, we should adopt an integrative approach that thoroughly assesses all the characteristics associated with expertise (see Determinants of Individual Variation in Expertise below). There is no doubt that expertise requires extensive practice, so it is not surprising that the effects of practice have dominated psychological analyses of expertise (Ericsson et al., 1993; Ericsson & Pool, 2016). An evolutionary biological analysis of expertise, however, requires us to broadly assess the functional and mechanistic bases of individual variation in all the characteristics that determine the acquisition rates and peak levels of expertise.

EXPERTISE IN OTHER SPECIES

Many carnivores attempt to capture prey that is similar to, or even exceeds, them in size, speed, power and cognitive abilities. As noted above for human hunting, capturing such prey is a highly complex task that requires integration of numerous cognitive and motor skills. A long-term study of wolves, *Canis lupus*, hunting moose, *Alces alces*, in the Scandinavian peninsula assessed major factors that

determined the predators' success rate. The wolf packs in Scandinavia typically consist of a breeding pair and their offspring. The young reach maximum body size and disperse in their first or second year. The age of the breeding male was the only significant predictor of moose hunting success, with males increasing their performance by over 50% from age 2 to age 5 (Fig. 2a). The effect of age was significant for males and not females most likely because males are about 30% larger than females and dominate moose hunting (Sand, Wikenros, Wabakken, & Liberg, 2006). Another long-term study of wolves hunting elk, *Cervus elaphus*, in Yellowstone National Park, U.S.A. focused on senescence but had relevant early life performance data. In that study, hunting success showed a large increase early in life, peaking at ages 2–3 years and then initiating a decline attributed to senescence (MacNulty et al., 2009). Finally, a long-term study of another carnivore, the spotted hyaena, *Crocuta crocuta*, also documented gradual increases in success rates of hunting large mammals with age, with success rates in solo hunts increasing from about 8% at age 3 to 50% at age 10 (Fig. 2b; Holekamp, Smale, Berg, & Cooper, 1997). Many bird studies have also reported a gradual increase in either foraging performance (Daunt, Afanasyev, Adam, Croxall, & Wanless, 2007; Desrochers, 1992; Fayet et al., 2015) or reproductive success (Leach & Sedinger, 2016; Reid, 1988; Wooler et al., 1990) with age, and the gradual accumulation of expertise is a primary explanation for that pattern.

Factors Other Than Experience

In addition to the effect of experience, other factors can explain increased performance with age. Such features have been addressed in a variety of studies. First, higher mortality rates of lesser quality individuals effectively create sample selection bias such that older individuals are of higher quality and hence show superior performance. For example, migratory performance of many birds shows apparent improvement with age when compared across individuals. In black kites, *Milvus migrans*, some of that change was indeed attributed to selective mortality. A within-individual comparison, however, revealed genuine individual improvement with age (Figure 2 in Sergio et al., 2014). Second, increased age may be associated with anatomical, morphological and physiological changes that enhance performance. Such changes, however, typically contribute to peak performance relatively soon after sexual maturity. For example, while hunting success in the Tsimane people of lowland Bolivia peaked around age 45, physical strength peaked in their late 20s and started to decline after age 30 (Gurven et al., 2006). Third, individuals may increase their effort with age. From a life history perspective, effort is the current investment into activities related to reproduction that reduces future survival or reproduction (Stearns, 1992). Both theory (Fagen, 1972; Roff, 2002; Taylor, 1991) and data (e.g. Hoffman, Higham, Mas-Rivera, Ayala, & Maestripieri, 2010; Pugesek, 1981; Reid, 1988; Yoccoz, Mysterud, Langvatn, & Stenseth, 2002) provide mixed findings about age-specific effort. Given the likely contribution of a few factors to the change in performance over time, it is sensible that we take a comprehensive approach when assessing the long-term effects of practice on performance.

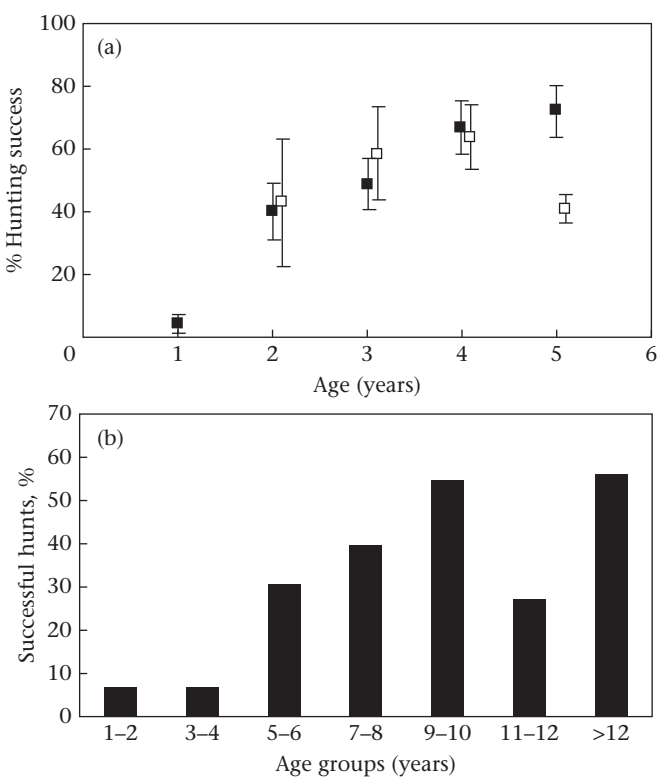

Figure 2. (a) The average ± SE successful moose hunts of male (black) and female (white) wolves as a function of their age. From Sand et al. (2006). (b) The percentage of successful solo hunts of large mammals as a function of age in spotted hyaenas. Data from Holekamp et al. (1997).

In my own laboratory's work, we indeed considered all the major factors that could explain the observed increase in foraging performance with experience in honey bees, *Apis mellifera* (Fig. 3). First, under natural settings, within-individual analyses indicated that bees' net rate of food delivery to the colony increased significantly with experience. Foraging performance doubled from the first day of foraging to the sixth day (Fig. 3a). The mean life span of foragers was only 7 days. These data are consistent with a large body of literature indicating that bees learn a variety of skills that can gradually improve their performance, including spatial orientation (Collett & Collett, 2002; Degen et al., 2016; Dyer, 1998) and flower handling (Durisko, Shipp, & Dukas, 2011; Laverty & Plowright, 1988; Reinhardt, 1952). The analysis across individuals, which also included foragers that lived longer than 7 days, revealed a similar pattern with the additional finding of a large decline in performance by older bees (Dukas & Visscher, 1994). In a follow-up study, we directly linked this decline to senescence (Dukas, 2008b). Second, to quantify physiological measures of performance, we analysed flight metabolic rates and flight muscle biochemistry throughout bees' life span. While bees had a large increase in measures of flight physiology before becoming foragers, they showed no further increase with foraging experience (Fig. 3b; Schippers, Dukas, & McClelland, 2010). Third, to assess the role of effort, we let bees collect 'nectar' from a feeder, a task that required little learning. Under these conditions, repeated measures of the same foragers indicated a performance increase over the bees' first few trips on day 1 but no further increase over 8 days (Fig. 3c; Dukas, 2008c). That is, there was no evidence for a gradual increase in performance at the feeder over several days. In contrast, bees foraging in challenging natural settings at the same location did show a gradual improvement over a few days (Dukas, 2008a). Overall, while we controlled for selection bias through repeated measures of the same individuals, bees showed a gradual increase in performance with experience. Complex skill acquisition was the only factor that could explain the results. Effort and physiology played negligible roles, except that physiology gradually declined, counteracting the increase in performance attributed to expertise.

MECHANISMS OF EXPERTISE

Expertise results from the effective integration of numerous heavily practiced tasks within a domain. It is thus possible that

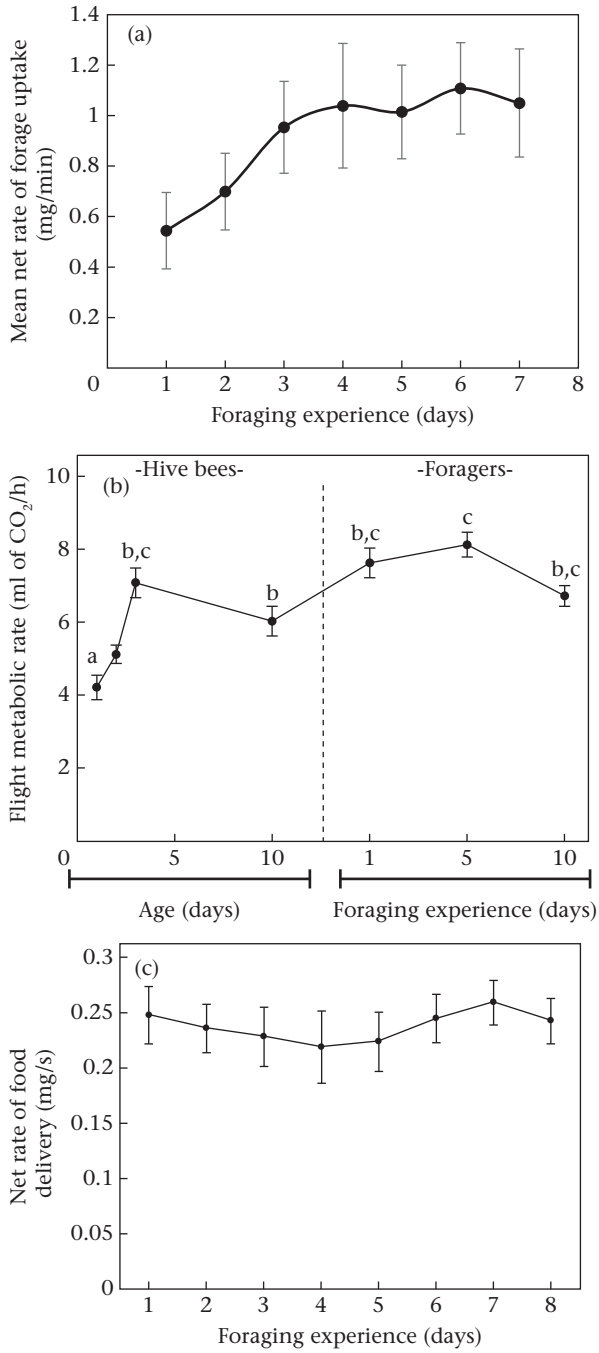

Figure 3. (a) Mean ± SE net rate of forage uptake as a function of the experience of honey bees foraging in natural settings. Data are based on individual averages of the same 27 bees that were active on each of the 7 days. Data from Dukas and Visscher (1994). (b) Mean ± SE hovering metabolic rates in honey bees as a function of their age and foraging experience. Adapted from Schippers et al. (2010). (c) Mean ± SE rate of food delivery as a function of the experience of honey bees foraging at a feeder providing 2.5 M sugar water. Means are based on individual averages of the same nine bees that were active on each of the 8 days. Data from Dukas (2008c).

expertise is merely the emergent property of extensive learning and memory. An examination of the major features of expertise (Table 1) indeed indicates that all may be the product of learning and memory. Learning can readily explain the greater long-term (Dudai, 1997; Landauer, 1986) and working memory (Ericsson & Kintsch, 1995) of experts. Attentional requirements on most tasks decrease with learning (Pashler, Johnston, & Ruthruff, 2001). Learning can allow one to anticipate certain events, focus attention on relevant features, comprehend a dynamic, complex scene and reach a decision quickly (Endsley, 2006). Finally, there is a well-known association between learning and superior motor control (Schmidt & Lee, 2011). A nonmutually exclusive alternative is that specific mechanisms enable the rapid, fluent, resourceful, well-coordinated, automatic-like action characterizing expert performance. Perhaps the top candidate mechanisms are the ones underlying chunking and automaticity.

Chunking involves organizing a set of elements into groups (chunks) based on known associations within each group (Gobet et al., 2001; Miller, 1956; Simon, 1974). Chunking can be quantified based on the fact that there is a stronger association within than between chunks. Hence in tests of memory recall, inter-item latency is shorter and inter-item accuracy is higher within than between chunks (e.g. Chase & Simon, 1973; Diedrichsen & Kornysheva, 2015; McLean & Gregg, 1967). Because chunking is based on familiarity, one can increase chunk size with experience. Chunking is important because it overcomes the severe limits of attention and working memory: we can devote little attention to familiar chunks, so larger chunks imply that we are free to attend to more information at any given time. Similarly, because working memory can hold only several items at any given time, larger chunks mean that we can better handle complex situations that require rapid evaluation of large amounts of information. Moreover, we can quickly scan and later accurately recall a set of chunks, but we require a much longer learning duration for memorizing with the same recall accuracy a set of unfamiliar groups with the same number of items (Fig. 4). Some studies have examined the neurobiological correlates of chunking (Diedrichsen & Kornysheva, 2015; Jin, Tecuapetla, & Costa, 2014; Matsuzaka, Picard, & Strick, 2007), but the exact mechanisms that enable it are not known. Similarly, several laboratories have documented that the development of expertise is associated with increased volumes of specific brain regions. Examples include exceptional navigators (Woollett & Maguire, 2011) and musicians (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Münte, Altenmüller, & Jäncke, 2002; Pantev et al., 1998). Such brain plasticity, however, has not been directly linked to chunking.

The development of expertise is accompanied by a gradual transition into task execution that requires substantially less attention and working memory. That is, while novices rely on slow, effortful cognitive processes, experts employ autonomous control (Anderson, 2000; Logan, 1988; Servant, Cassey, Woodman, & Logan, 2017; Shiffrin & Schneider, 1977). For example, when children learn basic addition, they start by the effortful process of successively incrementing a counter (e.g. Question: what is 3 + 2? Process → 3, 4, 5. Answer: 5). With experience, however, children can rapidly recall from long-term memory the answer (e.g. Question: what is 3 + 2? Answer: 5) (Ashcraft, 1982). Other highly familiar examples include the development of reading expertise, during which the identification of individual letters and many words becomes automatic (LaBerge & Samuels, 1974), and driving manual shift cars

(a) Animal expertise: mechanisms, ecology and evolution

(b) Ogtrcu oeaaxecie: lsdmetashn, pnomyli aiv neosnelmi

Figure 4. An example for chunking. The same letters are organized either into familiar chunks (a), or into randomly arranged letter-groups of similar length (b). The familiar chunks require less attention and working memory, and can be later recalled with higher accuracy than the random-letter groups.

discussed above (in the subsection, Features of Expertise). There has been relatively little neurobiological research on automatic processing (Servant et al., 2017; Vatansever, Menon, & Stamatakis, 2017; Yarrow, Brown, & Krakauer, 2009), and the mechanisms underlying it are unknown. It is possible that the extensive research on habit learning can provide insights into the mechanisms that produce automatic processing (Ashby, Turner, & Horvitz, 2010; Seger & Spiering, 2011; Yin & Knowlton, 2006).

As noted above, features of expertise including chunking and automatic processing may only be the emergent property of prolonged learning and the associated immense memory. Even in this feasible case, however, we need to explain the mechanisms that generate the brain's remarkable ability to integrate an enormous amount of information to produce expert performance. That is, the fact that learning more produces experts that (1) know more with no apparent upper limit to their knowledge base, (2) retrieve relevant information faster and (3) make superior decisions is not obvious. One can readily imagine an alternative, where learning new information results in forgetting older but still relevant information, memory interference, confusion and slower decisions. Indeed there is vast literature on memory interference under experimental conditions (Anderson, 2000; Spear & Riccio, 1994), but experts within their domain of expertise are resistant to such interference. That is, it is likely that, in addition to the heritable variation in traits such as learning and memory, individual variation in expertise is determined by heritable variation in additional features discussed in the next section.

DETERMINANTS OF INDIVIDUAL VARIATION IN EXPERTISE

We can gain a deeper understanding of the evolutionary biology of expertise from information about individual variation in the rate of expertise acquisition and peak performance, as well as the mechanisms that generate and maintain that variation. The prerequisite for expertise is extensive knowledge within a narrow discipline acquired over long periods of practice. Hence, traits influencing practice rate, learning rate and the organization and retention of memory must be important. A somewhat related, relevant, trait is perseverance, defined as persistence in a course of action despite difficulty or with little or no indication of success. Finally, expertise in domains requiring speed, endurance or power can be boosted by exceptional physiological, anatomical or morphological traits. I discuss these characteristics below and then follow with a synthesis.

Practice

If we compare same-age expert and novice adult humans, the most obvious difference between them is the amount of domain-specific practice. By mid-age, experts may have accumulated tens of thousands of hours of relevant experience while novices may have gained no pertinent knowledge. Indeed, in domains such as music performance and chess, there is a positive correlation between the amount of practice and level of expertise (Ericsson et al., 1993). While practice is necessary for expertise development, it is not sufficient. A necessary condition is that one is motivated to improve, attends to feedback and new relevant information and uses them to enhance subsequent performance (Ericsson et al., 1993; Ericsson & Pool, 2016). Two factors that increase the quality of practice in sports are making the task seem important and setting goals (Schmidt & Lee, 2011). In humans, coaches may provide such guidance, but parents or peers in many species can readily convey importance and goals. Parents, siblings and other conspecifics may also provide social facilitation through both encouragement and competitive interactions (Berger, 2016; Zajonc, 1965).

Although the positive correlation between the amount of practice and expertise is reassuring, it does not show causation. Nevertheless, controlled experiments on skill development, which typically assess relatively short-term improvement on a novel task, reveal a highly consistent, strong association between performance and practice. Performance shows an increasing, decelerating function that is well described by a simple power function, $P_e = aP_r{}^b$, where P_e is some relevant measure of performance, P_r is the amount of practice, and a and b are constants (Anderson, 2015; Newell & Rosenbloom, 1981; Schmidt & Lee, 2011). There are few controlled, long-term studies of skill development in nonhumans. A notable exception involves two baboons, *Papio papio*, trained with an increasingly large number of picture–response associations over 3.5 years and close to 300 000 training trials. The baboons reached a memory set size of about 6000 unique pictures with an average correct response of approximately 80%, much above the chance level of 50%. At that point, they showed no asymptote in their performance (Fagot & Cook, 2006). In short, practice combined with the ability and motivation to improve increases performance. As with most other organic traits (Polderman et al., 2015), individuals show heritable variation in traits influencing practice. For example, a large study involving over 10 000 Swedish twins reported heritability of 40–70% in individuals' inclination to practise music. An important feature affecting practice is perseverance, which is discussed next.

Perseverance

It seems challenging to persist when practice is difficult, and the hard work does not produce immediate apparent reward. Although both Darwin (1869, quoted in Galton, 1908) and Galton (1869) recognized the importance of zeal and hard work for achieving top performance, perseverance has received scant attention until recently (Duckworth, 2016; Duckworth, Peterson, Matthews, & Kelly, 2007; Fernald, 1912; Lufi & Cohen, 1987). It is probably helpful to make a clear distinction between perseverance and motivation. Motivation is a desire to do something to gain a reward. For example, one would expect a positive correlation between an individual's hunger level and its motivation to work to obtain food (Rolls, 2014). Perseverance means maintaining high levels of motivation and consequent work despite difficulties. For example, we would expect to find large individual variation in the number of attempts one directs towards attaining an attractive food item placed beyond a transparent barrier while controlling for obvious variables such as satiation and age. In humans, twin analyses indicate moderate heritability of 37% for perseverance and a high positive correlation with the related personality trait of conscientiousness (Rimfeld, Kovas, Dale, & Plomin, 2016). In nonhumans, there has been little research about perseverance, although a few studies have mentioned it, mostly in the context of succeeding in challenging tasks such as handling complex flowers (Heinrich, 1979; Muth, Keasar, & Dornhaus, 2015) or solving novel human-created problems (Griffin & Guez, 2014).

It is likely that perseverance is affected by individual variation in the internal rewards gained from practice, learning and tackling challenges. For example, both mice and humans show heritable variation in spontaneous physical activity (Garland et al., 2011; Stubbe & Geus, 2009). The internal rewards obtained from exercise such as running are mediated by dopamine and endocannabinoids (Fuss et al., 2015; Garland et al., 2011). Hence, genetic variation in the dopamine and endocannabinoid systems (Dincheva et al., 2015; Klein et al., 2007; Krugel, Biele, Mohr, Li, & Heekeren, 2009) can affect the magnitude of pleasure derived from conducting and improving on challenging physical and perhaps cognitive activities. Furthermore, genetic variation in pain perception (Mogil, 2012; Mogil et al., 1999; Nielsen et al., 2008) and

endogenous mechanisms of pain relief (Somogyi, Barratt, & Coller, 2007) can influence persistence in types of practice involving physical discomfort. Another key factor that determines an individual's ability to improve performance is its cognitive system, defined as the structures and processes concerned with the acquisition, retention and use of information (Dukas, 2004, 2017).

Cognitive Abilities

Individuals show moderate heritable variation in cognitive features. Studies in a variety of species from insects to mammals have documented heritable individual variation in learning (reviewed in Croston, Branch, Kozlovsky, Dukas, & Pravosudov, 2015; Dukas, 2004; Fuller & Thompson, 1978). In humans, the best available data are for intelligence, defined as the set of cognitive skills and knowledge associated with success in one's society (Hunt, 2010). A large body of literature indicates heritable individual variation in intelligence (Deary, 2012; Deary, Johnson, & Houlihan, 2009; Hunt, 2010; Plomin & Spinath, 2002). Similarly, there is heritable variation in both long-term memory (McClearn et al., 1997; Papassotiropoulos & de Quervain, 2011) and working memory (Ando, Ono, & Wright, 2001; Luciano et al., 2001; Posthuma et al., 2002). Heritable variation in traits linked to intelligence can be detected in infants. Moreover, infants' cognitive abilities in the first half year of life in the domains of attention, processing speed and memory are positively correlated with intelligence and academic achievement during childhood and young adulthood (Bornstein, 2014; Fagan, Holland, & Wheeler, 2007; McCall & Carriger, 1993; Rose, Feldman, & Jankowski, 2012). There are probably numerous single-nucleotide polymorphisms (SNPs) linked to intelligence, with each SNP contributing only a small fraction to the observed genetic variation. While several studies reported on SNPs linked to specific cognitive abilities, most of these findings have not been well replicated (Chabris et al., 2012, 2015; Plomin, Kennedy, & Craig, 2006).

Exceptional Physiology, Anatomy or Morphology

Young individuals developing a skill are more likely to persist if their success rate is high. One feature that can contribute to higher success is superior physiology, anatomy or morphology. In humans, there is moderate heritable variation in maximal oxygen uptake (VO_{2max}) and muscle strength and their responses to training, as well as anaerobic capacity, the relative proportions of skeletal muscle fibre types, and both motor performance and motor learning (Bouchard et al., 1998, 1999; Costa et al., 2012; Fox, Hershberger, & Bouchard, 1996; MacArthur & North, 2005; Tucker & Collins, 2012). Furthermore, allelic variation in over 200 genes has been linked to performance enhancement. Traits affected by these genes include blood flow to muscles, muscle structure, oxygen transport, lactate turnover and energy production and utilization (Gonzalez-Freire et al., 2009; MacArthur & North, 2005). For example, the human angiotensin-converting enzyme (*ACE*) gene has two common alleles. The insertion (*I*) allele is associated with lower activity of tissue ACE than the deletion (*D*) allele. A few studies have documented an excess of the *I* allele among elite endurance performers in both sports and high-altitude climbing (Berman & North, 2010; Montgomery et al., 1998; Myerson et al., 1999; Ostrander, Huson, & Ostrander, 2009). Furthermore, an experiment with British army recruits subjected to a 10-week physical training programme revealed an 11 times higher improvement in endurance in the *II* than *DD* carriers (Fig. 5) (Montgomery et al., 1998). Finally, it is important to note that extensive practice often leads to physiological, anatomical or morphological changes that contribute to superior expert performance. For example, tennis players have significantly greater bone mineral density in their playing arm than in their nonplaying arm compared to controls (Haapasalo et al., 2000; Huddleston, Rockwell, Kulund, & Harrison, 1980; Kannus et al., 1995). That is, there is synergy among the factors that contribute to expertise.

Synthesis

It is likely that complex interactions among the features discussed above determine individual variation in the attainment of expertise. Many types of expertise begin to develop early in life. Examples include song learning in songbirds, language acquisition in humans and hunting in carnivorous birds and mammals. Play in a variety of species can also contribute to the development of expertise (Bateson & Martin, 2013; Byers & Walker, 1995; Caro, 1988). Hence, individual variation in cognitive, motivational, physiological and physical features that is expressed early in life can translate into differences in individuals' responses to challenges and the consequent improvement trajectories. The simplest possibility is that an individual's objective or subjective assessment of its performance generates an internal feedback loop whereby perceived success encourages increased practice while failure leads to settling on less challenging undertakings. Similarly, variation

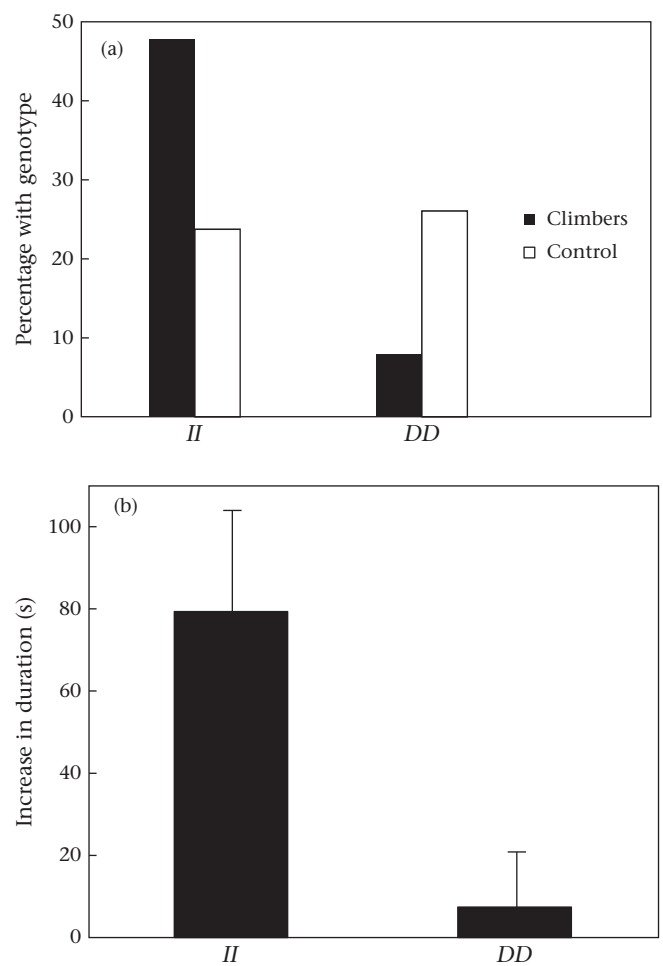

Figure 5. The association between the *I* and *D* alleles of the human angiotensin-converting enzyme (*ACE*) gene and athletic performance. (a) The distribution of the *ACE* alleles among 25 high-altitude climbers and 1906 control individuals. (b) Mean ± SE improvement in duration of repetitive elbow flexion after 10 weeks of training among British army recruits as a function of their *ACE* alleles. Data from Montgomery et al. (1998).

among young individuals can make them seek distinct physical or social environments that either promote their strengths or mask their weaknesses. In species with parental care, the parental environment as well as feedback from parents can create settings that contribute to enhanced performance. Some of these possibilities can be examined with the genotype–environment correlation approach from behavioural genetics, which distinguishes among three types of such correlation. Passive correlation refers to the fact that offspring and parents are genetically related and thus there can be a positive association between the offspring genotypes and the environment created by their parents. Reactive correlation means that reaction from the social environment depends on the offspring genotypes. Finally, active correlation implies that offspring seek an environment conducive to their genotype (Krapohl et al., 2017; Plomin, DeFries, & Loehlin, 1977). Edelaar, Siepielski, and Clobert (2008) term active correlation 'matching habitat choice' and discuss its evolutionary consequences.

CONCLUSIONS, PROSPECTS AND TESTABLE PREDICTIONS

Expertise has been studied for a few decades (e.g. Anderson, 1981; Bloom, 1985; Larkin, McDermont, Simon, & Simon, 1980; Simon & Chase, 1973), and explicit use of the term became prevalent late in the 20th Century (Chi, Glaser, & Farr, 1988; Ericsson & Lehmann, 1996; Ericsson & Smith, 1991). The research on expertise, however, has been primarily restricted to human subjects within the discipline of psychology, even though its relevance to nonhumans has long been appreciated (Dukas, 1998b; Helton, 2008). Is it possible that expertise is unique to humans? As discussed in the section on expertise in other species, fundamental biological considerations indicate that the same three general factors determine the age-specific performance in most animals (Dukas, 2008c; Stearns, 1992). The first factor is the gradual accumulation of skills and knowledge through learning. The second feature is the effort devoted to both performing a given task and to improving task execution. Finally, age-related changes in anatomy, morphology and physiology of relevant features can affect performance. These features typically reach peak at or soon after sexual maturity and later show slow, but accelerating, decline with ageing (Dukas, 2008c; Kirkwood & Austad, 2000; Rose, 1991). The combined outcome of the three factors generates a pattern of low performance early in life, high midlife achievement and a decline later in life. The exact age of peak performance and the magnitude of subsequent decline varies depending on the relative contributions of the three factors. For example, types of human expertise that require top speeds peak during the third decade of life, while kinds that rely on extensive experience and slow deliberation peak much later (Ericsson & Charness, 1994; Grossmann et al., 2010; Tanaka & Seals, 2008).

Analyses of expertise are relevant for most animals and we currently know of no neurobiological mechanism that is unique to human expertise. Nevertheless, it is possible that some features of expertise have a limited taxonomic distribution. First, by definition, expertise requires the acquisition of specific skills and knowledge that enable top performance on a complex task. This means that young individuals have to devote substantial time for expertise development. The majority of animals, however, have very short life spans, which severely limit the opportunity for mastering complex tasks. Moreover, young individuals in most species do not receive parental care, meaning that they cannot indulge in extensive practice while under parental provisioning and protection. Finally, parents are the most accessible and relevant source of social information, which can significantly boost expertise acquisition (Dukas, 2017). Only a small fraction of species, however, have parental care. That is, long-lived species with parental care can likely obtain high levels of expertise distinct from those of short-lived species with no parental care.

The likelihood that long-lived species with parental care can attain superior levels of expertise leads to a related, second possibility. Selection pressures associated with increased life span, parental care and the greater opportunities to acquire expertise may have led to the evolution of unique mechanisms of expertise. Indeed, two whole genome duplication events early in the evolution of vertebrates (Putnam et al., 2008) have led to gene expansion in many synaptic gene families and expanded neuronal complexity in that lineage (Emes & Grant, 2012; Ryan & Grant, 2009; Van de Peer, Maere, & Meyer, 2009). Hence, we will need to conduct comparative experimental analyses to find out whether some mechanisms of expertise are unique to a limited range of taxa. Regardless of the outcomes of such analyses, it is important that we appreciate the fact that even species that live relatively short lives still have ample opportunities to acquire expertise. We cannot, however, assess peak expert performance if we do not allow individuals the time and opportunities to acquire their expertise, which must be linked to their natural history. That is, if we either test only young individuals or use an artificial laboratory protocol, we may grossly underestimate a species' ability. Hence we should devote more research effort to quantifying the development of expertise by individuals in their natural settings.

Prospects and Testable Predictions

The field of animal behaviour can benefit from a concentrated effort devoted to research on the mechanisms, ecology and evolutionary biology of expertise as well as the effects of expertise on animal ecology and evolution. On the mechanistic side, a promising research direction involves the dramatic changes in information processing with skill acquisition. While terms such as chunking and automaticity have been used for decades (see Mechanisms of Expertise), we do not understand the neurobiological mechanisms that generate them. There has been insightful research on mechanisms of chunking in animal models such as monkeys and mice (Jin et al., 2014; Matsuzaka et al., 2007). Perhaps, however, a more fruitful approach would be to focus on simpler and more trackable model systems such as fruit flies or bees. On the evolutionary ecological side, the main inquiry should involve quantifying genetic variation in the rates of expertise acquisition and peak performance, and their fitness consequences. This can also lead to genomic and neurobiological work on the mechanisms that generate expertise.

Aspects of expertise reviewed above are relevant to many research areas in animal behaviour. Hence, using the expertise approach can generate insightful research directions. I will illustrate this with three examples. First, there has been substantial research on the adaptive use of spatial memory in food-caching birds (e.g. Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Pravosudov & Roth, 2013). It is likely that, with practice, individual birds become experts at seed caching and retrieval. That is, I propose that there will be a positive correlation between a bird's age and the proportion of cached, marked seeds that it retrieves. Second, while issues of learning, intelligence and brain size have been studied extensively in animal behaviour, perseverance has received little attention. Persistent, high-quality practice, however, is essential for expertise development. We should thus address questions regarding heritable individual variation in perseverance and its effects on fitness. Besides the intuitive prediction that perseverance will be positively associated with relevant measures of success, one can imagine more nuanced possibilities whereby perseverance is a highly plastic trait that varies based on expected benefits and costs that differ among individuals and environments. For example, it may not be optimal for individuals of either low quality or expected short life span to

persevere in expertise development (see Daly & Wilson, 2005; Réale et al., 2010). Finally, research on animal groups and their social interactions has been highly illuminating (e.g. Allee, 1931; Krause & Ruxton, 2002; Ward & Webster, 2016). An intriguing phenomenon in human social groups that is highly relevant to other species is the development of group expertise. That is, when individuals are placed together, for example, in a factory assembly line, they show a gradual improvement in performance measures including increases in production rates and product quality and a decrease in accident rates. At least some of this enhancement can be attributed to changes in communication and social dynamics that enhance coordination and efficiency of the production process (Argote & Epple, 1990). Such a pattern has not been documented in nonhuman species but can be highly relevant for species that form long-lasting groups. In such species, I expect to find a long-term improvement in measures such as group hunting success and injury rates.

Research on expertise can also provide ecological and evolutionary insights. Many species consist of individuals whose niches are small subsets of the population niche. There has recently been increased interest in understanding the causes and consequences of such within-species variation in niche (Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2003, 2011; Ingram, Costa-Pereira, & Araújo, 2018; Wennersten & Forsman, 2012). At least three aspects of expertise are major contributors to individual variation in niche. First, expertise often implies specialization because it takes a long time and extensive practice to develop. Second, variation in cumulative practice, which is moderately positively correlated with age, generates wide individual variation in measures of performance. Third, individual variation in traits determining expertise including learning ability, working memory capacity and perseverance, generates individual variation in expertise. Hence, examining the effects of expertise on individual variation in niche can help us understand ecological and evolutionary dynamics. Furthermore, studying expertise can help us understand the evolution of cognitive abilities and intelligence. Selection on greater expertise may have led to a positive evolutionary feedback enhancing cognitive traits and altering life history characteristics. Because greater expertise can lead to greater fitness, there may have been selection for longer life spans, which allow more time for attaining expertise. In turn, longer life may have increased the value of investment in structures that enable greater expertise as well as providing, through parental care, the time, resources and safety that allow offspring to initiate expertise acquisition (Dukas, 2017).

In summary, expertise acquisition is a major yet neglected animal life history trait. Both expert performance and the features associated with it can be well characterized and quantified. Future work should focus on heritable variation in mechanisms that determine expertise acquisition and peak performance, the neurobiological mechanisms that enable expertise, the fitness consequences of traits contributing to top expert performance and the ecological and evolutionary consequences of expertise.

Acknowledgments

I thank L. Dukas for assistance, P. Andrews, L. Dukas, S. Phelps, A. Thomson, participants of the Animal Behaviour Discussion Group in Ottawa and two anonymous referees for comments on the manuscript, and the Natural Sciences and Engineering Research Council of Canada, Canada Foundation for Innovation and Ontario Ministry of Research and Innovation for funding.

References

Allee, W. C. (1931). *Animal aggregations. A study in general sociology*. Chicago, IL: University of Chicago Press.

Anderson, J. R. (1981). *Cognitive skills and their acquisition*. Hillsdale, NJ: L. Earlbaum.

Anderson, J. R. (2000). *Learning and memory*. New York, NY: J. Wiley.

Anderson, J. R. (2015). *Cognitive psychology and its implications* (8th ed.). New York, NY: MacMillan.

Ando, J., Ono, Y., & Wright, M. J. (2001). Genetic structure of spatial and verbal working memory. *Behavior Genetics, 31*, 615–624.

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters, 14*, 948–958.

Argote, L., & Epple, D. (1990). Learning curves in manufacturing. *Science, 247*, 920–924.

Ashby, F. G., Turner, B. O., & Horvitz, J. C. (2010). Cortical and basal ganglia contributions to habit learning and automaticity. *Trends in Cognitive Sciences, 14*, 208–215.

Ashcraft, M. H. (1982). The development of mental arithmetic: A chronometric approach. *Developmental Review, 2*, 213–236.

Bateson, P., & Martin, P. (2013). *Play, playfulness, creativity and innovation*. Cambridge, U.K.: Cambridge University Press.

Berger, J. (2016). *Invisible influence: The hidden forces that shape behavior*. New York, NY: Simon & Schuster.

Berman, Y., & North, K. N. (2010). A gene for speed: The emerging role of α-actinin-3 in muscle metabolism. *Physiology, 25*, 250–259.

Birkmeyer, J. D., Siewers, A. E., Finlayson, E. V. A., Stukel, T. A., Lucas, F. L., Batista, I., et al. (2002). Hospital volume and surgical mortality in the United States. *New England Journal of Medicine, 346*, 1128–1137.

Bloom, B. S. (1985). *Developing talent in young people*. New York, NY: Ballantine.

Blurton Jones, N., & Marlowe, F. W. (2002). Selection for delayed maturity. *Human Nature, 13*, 199–238.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., et al. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution, 26*, 183–192.

Bolnick, D. I., Svanback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., et al. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist, 161*, 1–28.

Bornstein, M. H. (2014). Human infancy… and the rest of the lifespan. *Annual Review of Psychology, 65*, 121–158.

Bor, D., & Owen, A. M. (2007). A common prefrontal–parietal network for mnemonic and mathematical recoding strategies within working memory. *Cerebral Cortex, 17*, 778–786.

Bouchard, C., An, P., Rice, T., Skinner, J. S., Wilmore, J. H., Gagnon, J., et al. (1999). Familial aggregation of VO_{2max}; Response to exercise training: Results from the Heritage family study. *Journal of Applied Physiology, 87*, 1003.

Bouchard, C., Daw, E. W., Rice, T., Pérusse, L., Gagnon, J., Province, M. A., et al. (1998). Familial resemblance for VO_{2max} in the sedentary state: The Heritage family study. *Medicine and Science in Sports and Exercise, 30*, 252–258.

Bridgewater, B., Grayson, A. D., Au, J., Hassan, R., Dihmis, W. C., Munsch, C., et al. (2004). Improving mortality of coronary surgery over first four years of independent practice: Retrospective examination of prospectively collected data from 15 surgeons. *BMJ, 329*, 421–423.

Bull, C., Yates, R., Sarkar, D., Deanfield, J., & de Leval, M. (2000). Scientific, ethical, and logistical considerations in introducing a new operation: A retrospective cohort study from paediatric cardiac surgery. *BMJ, 320*, 1168.

Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *American Naturalist, 146*, 25–40.

Calderwood, R., Klein, G. A., & Crandall, B. W. (1988). Time pressure, skill, and move quality in chess. *American Journal of Psychology, 101*, 481–493.

Caro, T. M. (1988). Adaptive significance of play: Are we getting closer? *Trends in Ecology & Evolution, 3*, 50–54.

Chabris, C. F., Hebert, B. M., Benjamin, D. J., Beauchamp, J., Cesarini, D., van der Loos, M., et al. (2012). Most reported genetic associations with general intelligence are probably false positives. *Psychological Science, 23*, 1314–1323.

Chabris, C. F., Lee, J. J., Cesarini, D., Benjamin, D. J., & Laibson, D. I. (2015). The fourth law of behavior genetics. *Current Directions in Psychological Science, 24*, 304–312.

Chase, W. G., & Simon, H. A. (1973). Perception in chess. *Cognitive Psychology, 4*, 55–81.

Chi, M. T., Glaser, R. E., & Farr, M. (1988). *The nature of expertise*. Hillsdale, NJ: L. Erlbaum.

Clark, E. V. (2009). *First language acquisition*. Cambridge, U.K.: Cambridge University Press.

Collett, T. S., & Collett, M. (2002). Memory use in insect visual navigation. *Nature Reviews Neuroscience, 3*, 542–552.

Costa, A. M., Breitenfeld, L., Silva, A. J., Pereira, A., Izquierdo, M., & Marques, M. C. (2012). Genetic inheritance effects on endurance and muscle strength. *Sports Medicine, 42*, 449–458.

Croston, R., Branch, C. L., Kozlovsky, D. Y., Dukas, R., & Pravosudov, V. V. (2015). Heritability and the evolution of cognitive traits. *Behavioral Ecology, 26*, 1447–1459.

Daly, M., & Wilson, M. (2005). Carpe diem: Adaptation and devaluing the future. *Quarterly Review of Biology, 80*, 55–60.

Daunt, F., Afanasyev, V., Adam, A., Croxall, J. P., & Wanless, S. (2007). From cradle to early grave: Juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters, 3*, 371–374.

De Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): A perception–action perspective. *Developmental Science, 11*, 828–840.

Deary, I. J. (2012). Intelligence. *Annual Review of Psychology, 63*, 453–482.
Deary, I. J., Johnson, W., & Houlihan, L. M. (2009). Genetic foundations of human intelligence. *Human Genetics, 126*, 215–232.
Degen, J., Kirbach, A., Reiter, L., Lehmann, K., Norton, P., Storms, M., et al. (2016). Honeybees learn landscape features during exploratory orientation flights. *Current Biology, 26*, 2800–2804.
Desrochers, A. (1992). Age and foraging success in European blackbirds: Variation between and within individuals. *Animal Behaviour, 43*, 885–894.
Diedrichsen, J., & Kornysheva, K. (2015). Motor skill learning between selection and execution. *Trends in Cognitive Sciences, 19*, 227–233.
Dincheva, I., Drysdale, A. T., Hartley, C. A., Johnson, D. C., Jing, D., King, E. C., et al. (2015). FAAH genetic variation enhances fronto-amygdala function in mouse and human. *Nature, 6*, 6395. https://doi.org/10.1038/ncomms7395.
Duckworth, A. (2016). *Grit: The power of passion and perseverance*. New York, NY: Scribner.
Duckworth, A. L., Peterson, C., Matthews, M. D., & Kelly, D. R. (2007). Grit: Perseverance and passion for long-term goals. *Journal of Personality and Social Psychology, 92*, 1087–1101.
Dudai, Y. (1997). How big is human memory, or on being just useful enough. *Learning & Memory, 3*, 341–365.
Dukas, R. (1998a). Introduction. In R. Dukas (Ed.), *Cognitive ecology* (pp. 1–19). Chicago, IL: University of Chicago Press.
Dukas, R. (1998b). Evolutionary ecology of learning. In R. Dukas (Ed.), *Cognitive ecology* (pp. 129–174). Chicago, IL: University of Chicago Press.
Dukas, R. (2002). Behavioural and ecological consequences of limited attention. *Philosophical Transactions of the Royal Society B, 357*, 1539–1548.
Dukas, R. (2004). Evolutionary biology of animal cognition. *Annual Review of Ecology, Evolution, and Systematics, 35*, 347–374.
Dukas, R. (2008a). Life history of learning: Performance curves of honeybees in the wild. *Ethology, 114*, 1195–1200.
Dukas, R. (2008b). Bee senescence in the wild. *Insectes Sociaux, 55*, 252–255.
Dukas, R. (2008c). Life history of learning: Performance curves of honeybees in settings that minimize the role of learning. *Animal Behaviour, 75*, 1125–1130.
Dukas, R. (2009). Learning: Mechanisms, ecology and evolution. In R. Dukas, & J. Ratcliffe (Eds.), *Cognitive ecology II* (pp. 7–30). Chicago, IL: University of Chicago Press.
Dukas, R. (2017). Cognitive innovations and the evolutionary biology of expertise. *Philosophical Transactions of the Royal Society B, 372*, 20160427.
Dukas, R., & Visscher, P. K. (1994). Lifetime learning by foraging honey bees. *Animal Behaviour, 48*, 1007–1012.
Durisko, Z., Shipp, L., & Dukas, R. (2011). Effects of experience on short- and long-term foraging performance in bumblebees. *Ethology, 117*, 49–55.
Dyer, F. C. (1998). Cognitive ecology of navigation. In R. Dukas (Ed.), *Cognitive ecology* (pp. 201–260). Chicago, IL: University of Chicago Press.
Edelaar, P., Siepielski, A. M., & Clobert, J. (2008). Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology. *Evolution, 62*, 2462–2472.
Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science, 270*, 305–307.
Emes, R. D., & Grant, S. G. N. (2012). Evolution of synapse complexity and diversity. *Annual Review of Neuroscience, 35*, 111–131.
Endsley, M. R. (2006). Expertise and situation awareness. In K. A. Ericsson, N. Charness, P. J. Feltovich, & R. R. Hoffman (Eds.), *The Cambridge handbook of expertise and expert performance* (pp. 633–651). Cambridge, U.K.: Cambridge University Press.
Endsley, M. R., & Jones, D. G. (2004). *Designing for situation awareness: An approach to user-centered design*. Boca Raton, FL: CRC Press.
Ericsson, K. A., & Charness, N. (1994). Expert performance: Its structure and acquisition. *American Psychologist, 49*, 725–747.
Ericsson, K. A., Charness, N., Feltovich, P. J., & Hoffman, R. R. (2006). *The Cambridge handbook of expertise and expert performance*. Cambridge, U.K.: Cambridge University Press.
Ericsson, K. A., & Kintsch, W. (1995). Long-term working memory. *Psychological Review, 102*, 211–245.
Ericsson, K. A., Krampe, R. T., & Tesch-Römer, C. (1993). The role of deliberate practice in the acquisition of expert performance. *Psychological Review, 100*, 363–406.
Ericsson, K. A., & Lehmann, A. C. (1996). Expert and exceptional performance: Evidence of maximal adaptation to task constraints. *Annual Review of Psychology, 47*, 273–305.
Ericsson, A., & Pool, R. (2016). *Peak: Secrets from the new science of expertise*. Boston, MA: Houghton Mifflin Harcourt.
Ericsson, K. A., & Smith, J. (1991). *Toward a general theory of expertise: Prospects and limits*. Cambridge, U.K.: Cambridge University Press.
Fabre, J.-H., Teixeira de Mattos, A., & Miall, B. (1918). *The wonders of instinct*. New York, NY: Century.
Fagan, J. F., Holland, C. R., & Wheeler, K. (2007). The prediction, from infancy, of adult IQ and achievement. *Intelligence, 35*, 225–231.
Fagen, R. M. (1972). An optimal life history strategy in which reproductive effort decreases with age. *American Naturalist, 106*, 258–261.
Fagot, J., & Cook, R. G. (2006). Evidence for large long-term memory capacities in baboons and pigeons and its implications for learning and the evolution of cognition. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 17564–17567.
Fayet, A. L., Freeman, R., Shoji, A., Padget, O., Perrins, C. M., & Guilford, T. (2015). Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird. *Animal Behaviour, 110*, 79–89.
Fernald, G. G. (1912). An achievement capacity test: A preliminary report. *Journal of Educational Psychology, 3*, 331–336.
Fox, P. W., Hershberger, S. L., & Bouchard, T. J., Jr. (1996). Genetic and environmental contributions to the acquisition of a motor skill. *Nature, 384*, 356–358.
Fuller, J. L., & Thompson, W. R. (1978). *Foundations of behavior genetics*. St Louis, MO: Mosby.
Fuss, J., Steinle, J., Bindila, L., Auer, M. K., Kirchherr, H., Lutz, B., et al. (2015). A runner's high depends on cannabinoid receptors in mice. *Proceedings of the National Academy of Sciences of the United States of America, 112*, 13105–13108.
Galton, F. (1869). *Hereditary genius: An inquiry into its laws and consequences*. London, U.K.: Macmillan.
Galton, F. (1908). *Memories of my life*. London, U.K.: Methuen.
Garland, T., Jr., Schutz, H., Chappell, M. A., Keeney, B. K., Meek, T. H., Copes, L. E., et al. (2011). The biological control of voluntary exercise, spontaneous physical activity and daily energy expenditure in relation to obesity: Human and rodent perspectives. *Journal of Experimental Biology, 214*, 206–229.
Gawande, A. (2002). The learning curve. *New Yorker, 77*, 52–61.
Gobet, F., Lane, P. C. R., Croker, S., Cheng, P. C. H., Jones, G., Oliver, I., et al. (2001). Chunking mechanisms in human learning. *Trends in Cognitive Sciences, 5*, 236–243.
Gobet, F., & Simon, H. A. (1996). Recall of rapidly presented random chess positions is a function of skill. *Psychonomic Bulletin & Review, 3*, 159–163.
Gonzalez-Freire, M., Santiago, C., Verde, Z., Lao, J. I., Oiivan, J., Gómez-Gallego, F., et al. (2009). Unique among unique. Is it genetically determined? *British Journal of Sports Medicine, 43*, 307–309.
González-Ruibal, A., Hernando, A., & Politis, G. (2011). Ontology of the self and material culture: Arrow-making among the Awá hunter–gatherers (Brazil). *Journal of Anthropological Archaeology, 30*, 1–16.
Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes, 109*, 121–134.
Grossmann, I., Na, J., Varnum, M. E. W., Park, D. C., Kitayama, S., & Nisbett, R. E. (2010). Reasoning about social conflicts improves into old age. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 7246–7250.
Gurven, M., & Kaplan, H. (2006). Determinants of time allocation across the lifespan: A theoretical model and an application to the Machiguenga and Piro of Peru. *Human Nature, 17*, 1–49.
Gurven, M., Kaplan, H., & Gutierrez, M. (2006). How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *Journal of Human Evolution, 51*, 454–470.
Haapasalo, H., Kontulainen, S., Sievänen, H., Kannus, P., Järvinen, M., & Vuori, I. (2000). Exercise-induced bone gain is due to enlargement in bone size without a change in volumetric bone density: A peripheral quantitative computed tomography study of the upper arms of male tennis players. *Bone, 27*, 351–357.
Heckman, J. J. (1979). Sample selection bias as a specification error. *Econometrica, 47*, 153–161.
Heinrich, B. (1979). Majoring and minoring by foraging bumblebees, *Bombus vagance*: An experimental analysis. *Ecology, 60*, 245–255.
Helton, W. S. (2008). Expertise acquisition as sustained learning in humans and other animals: Commonalities across species. *Animal Cognition, 11*, 99–107.
Hoffman, C. L., Higham, J. P., Mas-Rivera, A., Ayala, J. E., & Maestripieri, D. (2010). Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. *Behavioral Ecology, 21*, 972–978.
Holekamp, K. E., Smale, L., Berg, R., & Cooper, S. M. (1997). Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology, 242*, 1–15.
Huddleston, A. L., Rockwell, D., Kulund, D. N., & Harrison, R. (1980). Bone mass in lifetime tennis athletes. *JAMA, 244*, 1107–1109.
Hunt, E. (2010). *Human intelligence*. Cambridge, U.K.: Cambridge University Press.
Ingram, T., Costa-Pereira, R., & Araújo, M. S. (2018). The dimensionality of individual niche variation. *Ecology, 99*, 536–549.
Jin, X., Tecuapetla, F., & Costa, R. M. (2014). Basal ganglia subcircuits distinctively encode the parsing and concatenation of action sequences. *Nature Neuroscience, 17*, 423–430.
Kannus, P., Haapasalo, H., Sankelo, M., Sievanen, H., Pasanen, M., Heinonen, A., et al. (1995). Effect of starting age of physical activity on bone mass in the dominant arm of tennis and squash players. *Annals of Internal Medicine, 123*, 27–31.
Kirkwood, T. B. L., & Austad, S. N. (2000). Why do we age? *Nature, 408*, 233–238.
Klein, T. A., Neumann, J., Reuter, M., Hennig, J., von Cramon, D. Y., & Ullsperger, M. (2007). Genetically determined differences in learning from errors. *Science, 318*, 1642–1645.
Krampe, R. T., Engbert, R., & Kliegl, R. (2002). The effects of expertise and age on rhythm production: Adaptations to timing and sequencing constraints. *Brain and Cognition, 48*, 179–194.
Krapohl, E., Hannigan, L. J., Pingault, J.-B., Patel, H., Kadeva, N., Curtis, C., et al. (2017). Widespread covariation of early environmental exposures and trait-associated polygenic variation. *Proceedings of the National Academy of Sciences of the United States of America, 114*, 11727–11732.
Krause, J., & Ruxton, G. (2002). *Living in groups*. Oxford, U.K.: Oxford University Press.
Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H., & Vaccarino, A. L. (1989). Hippocampal specialization in food-storing birds. *Proceedings of the National Academy of Sciences of the United States of America, 86*, 1388–1392.

Krugel, L. K., Biele, G., Mohr, P. N. C., Li, S.-C., & Heekeren, H. R. (2009). Genetic variation in dopaminergic neuromodulation influences the ability to rapidly and flexibly adapt decisions. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 17951–17956.
LaBerge, D., & Samuels, S. J. (1974). Toward a theory of automatic processing in reading. *Cognitive Psychology, 6*, 293–323.
Landauer, T. K. (1986). How much do people remember? Some estimates of the quantity of learned information in long-term memory. *Cognitive Science, 10*, 477–493.
Larkin, J., McDermont, J., Simon, D. P., & Simon, H. A. (1980). Expert and novice performance in solving physics problems. *Science, 208*, 1335–1342.
Laverty, T. M., & Plowright, R. C. (1988). Flower handling by bumblebees: A comparison of specialists and generalists. *Animal Behaviour, 36*, 733–740.
Leach, A. G., & Sedinger, J. S. (2016). Male breeding experience, not mate familiarity, affects reproductive output in black brant geese. *Behavioral Ecology, 27*, 1851–1858.
Liebenberg, L., Louw, A., & Elbroch, M. (2010). *Practical tracking: A guide to following footprints and finding animals*. Mechanicsburg, PA: Stackpole.
Logan, G. D. (1988). Toward an instance theory of automatization. *Psychological Review, 95*, 492–527.
Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour, 70*, 673–683.
Lothrop, S. K. (1928). *The Indians of Tierra del Fuego*. New York, NY: Museum of the American Indian.
Luciano, M., Wright, M. J., Smith, G. A., Geffen, G. M., Geffen, L. B., & Martin, N. G. (2001). Genetic covariance among measures of information processing speed, working memory, and IQ. *Behavior Genetics, 31*, 581–592.
Lufi, D., & Cohen, A. (1987). A scale for measuring persistence in children. *Journal of Personality Assessment, 51*, 178–185.
MacArthur, D. G., & North, K. N. (2005). Genes and human elite athletic performance. *Human Genetics, 116*, 331–339.
MacDonald, K. (2007). Cross-cultural comparison of learning in human hunting. *Human Nature, 18*, 386–402.
MacNulty, D. R., Smith, D. W., Vucetich, J. A., Mech, L. D., Stahler, D. R., & Packer, C. (2009). Predatory senescence in ageing wolves. *Ecology Letters, 12*, 1347–1356.
Matsuzaka, Y., Picard, N., & Strick, P. L. (2007). Skill representation in the primary motor cortex after long-term practice. *Journal of Neurophysiology, 97*, 1819–1832.
McCall, R. B., & Carriger, M. S. (1993). A meta-analysis of infant habituation and recognition memory performance as predictors of later IQ. *Child Development, 64*, 57–79.
McClearn, G. E., Johansson, B., Berg, S., Pedersen, N. L., Ahern, F., Petrill, S. A., et al. (1997). Substantial genetic influence on cognitive abilities in twins 80 or more years old. *Science, 276*, 1560–1563.
McLean, R., & Gregg, L. (1967). Effects of induced chunking on temporal aspects of serial recitation. *Journal of Experimental Psychology, 74*, 455–459.
Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review, 63*, 81–97.
Mogil, J. S. (2012). Pain genetics: Past, present and future. *Trends in Genetics, 28*, 258–266.
Mogil, J. S., Wilson, S. G., Bon, K., Eun Lee, S., Chung, K., Raber, P., et al. (1999). Heritability of nociception I: Responses of 11 inbred mouse strains on 12 measures of nociception. *Pain, 80*, 67–82.
Montgomery, H., Marshall, R., Hemingway, H., Myerson, S., Clarkson, P., Dollery, C., et al. (1998). Human gene for physical performance. *Nature, 393*, 221–222.
Münte, T. F., Altenmüller, E., & Jäncke, L. (2002). The musician's brain as a model of neuroplasticity. *Nature Reviews Neuroscience, 3*, 473–478.
Muth, F., Keasar, T., & Dornhaus, A. (2015). Trading off short-term costs for long-term gains: How do bumblebees decide to learn morphologically complex flowers? *Animal Behaviour, 101*, 191–199.
Myerson, S., Hemingway, H., Budget, R., Martin, J., Humphries, S., & Montgomery, H. (1999). Human angiotensin I-converting enzyme gene and endurance performance. *Journal of Applied Physiology, 87*, 1313–1316.
Newell, A., & Rosenbloom, P. S. (1981). Mechanisms of skill acquisition and the law of practice. In J. R. Anderson (Ed.), *Cognitive skills and their acquisition* (pp. 1–55). Hillsdale, NJ: L. Erlbaum.
Nielsen, C. S., Stubhaug, A., Price, D. D., Vassend, O., Czajkowski, N., & Harris, J. R. (2008). Individual differences in pain sensitivity: Genetic and environmental contributions. *Pain, 136*, 21–29.
Ohtsuka, R. (1989). Hunting activity and aging among the Gidra Papuans: A biobehavioral analysis. *American Journal of Physical Anthropology, 80*, 31–39.
Ostrander, E. A., Huson, H. J., & Ostrander, G. K. (2009). Genetics of athletic performance. *Annual Review of Genomics and Human Genetics, 10*, 407–429.
Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L. E., & Hoke, M. (1998). Increased auditory cortical representation in musicians. *Nature, 392*, 811–814.
Papassotiropoulos, A., & de Quervain, D. J. F. (2011). Genetics of human episodic memory: Dealing with complexity. *Trends in Cognitive Sciences, 15*, 381–387.
Pashler, H., Johnston, J. C., & Ruthruff, E. (2001). Attention and performance. *Annual Review of Psychology, 52*, 629–651.
Plomin, R., DeFries, J. C., & Loehlin, J. C. (1977). Genotype–environment interaction and correlation in the analysis of human behavior. *Psychological Bulletin, 84*, 309–322.
Plomin, R., Kennedy, J. K. J., & Craig, I. W. (2006). The quest for quantitative trait loci associated with intelligence. *Intelligence, 34*, 513–526.
Plomin, R., & Spinath, F. M. (2002). Genetics and general cognitive ability (g). *Trends in Cognitive Sciences, 6*, 169–176.
Polderman, T. J. C., Benyamin, B., de Leeuw, C. A., Sullivan, P. F., van Bochoven, A., Visscher, P. M., et al. (2015). Meta-analysis of the heritability of human traits based on fifty years of twin studies. *Nature Genetics, 47*, 702–709.
Posthuma, D., De Geus, E. J. C., Baare, W. F. C., Pol, H. E. H., Kahn, R. S., & Boomsma, D. I. (2002). The association between brain volume and intelligence is of genetic origin. *Nature Neuroscience, 5*, 83–84.
Pravosudov, V. V., & Roth, T. C. (2013). Cognitive ecology of food hoarding: The evolution of spatial memory and the hippocampus. *Annual Review of Ecology, Evolution, and Systematics, 44*, 173–193.
Pugesek, B. H. (1981). Increased reproductive effort with age in the California gull (*Larus californicus*). *Science, 212*, 822–823.
Putnam, N. H., Butts, T., Ferrier, D. E. K., Furlong, R. F., Hellsten, U., Kawashima, T., et al. (2008). The amphioxus genome and the evolution of the chordate karyotype. *Nature, 453*, 1064–1071.
Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*, 4051–4063.
Reid, W. V. (1988). Age-specific patterns of reproduction in the glaucous-winged gull: Increased effort with age? *Ecology, 69*, 1454–1465.
Reinhardt, J. F. (1952). Some responses of honey bees to alfalfa flowers. *American Naturalist, 86*, 257–275.
Richards, R. J. (1987). *Darwin and the emergence of evolutionary theories of mind and behavior*. Chicago, IL: University of Chicago Press.
Rimfeld, K., Kovas, Y., Dale, P. S., & Plomin, R. (2016). True grit and genetics: Predicting academic achievement from personality. *Journal of Personality and Social Psychology, 111*, 780.
Roff, D. A. (2002). *Life history evolution*. Sunderland, MA: Sinauer.
Rolls, E. T. (2014). *Emotion and decision-making explained*. Oxford, U.K.: Oxford University Press.
Rose, M. R. (1991). *Evolutionary biology of aging*. New York, NY: Oxford University Press.
Rose, S. A., Feldman, J. F., & Jankowski, J. J. (2012). Implications of infant cognition for executive functions at age 11. *Psychological Science, 23*, 1345–1355.
Rutz, C. (2012). Predator fitness increases with selectivity for odd prey. *Current Biology, 22*, 820–824.
Ryan, T. J., & Grant, S. G. N. (2009). The origin and evolution of synapses. *Nature Reviews Neuroscience, 10*, 701–712.
Sand, H., Wikenros, C., Wabakken, P., & Liberg, O. (2006). Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour, 72*, 781–789.
Schippers, M.-P., Dukas, R., & McClelland, G. B. (2010). Lifetime changes in flight metabolic rate and muscle biochemistry of honeybees, *Apis mellifera*. *Journal of Comparative Physiology B, 180*, 45–55.
Schmidt, R., & Lee, T. (2011). *Motor control and learning: A behavioral emphasis* (5th ed.). Champaign, IL: Human Kinetics.
Seger, C., & Spiering, B. (2011). A critical review of habit learning and the basal ganglia. *Frontiers in Systems Neuroscience, 5*, 66. https://doi.org/10.3389/fnsys.2011.00066.
Sergio, F., Tanferna, A., De Stephanis, R., Jimenez, L. L., Blas, J., Tavecchia, G., et al. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature, 515*, 410–413.
Servant, M., Cassey, P., Woodman, G., & Logan, G. (2017). Neural bases of automaticity. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 44*(3), 440–464.
Shaw, M. L., & Shaw, P. (1977). Optimal allocation of cognitive resources to spatial locations. *Journal of Experimental Psychology: Human Perception and Performance, 3*, 201–211.
Shettleworth, S. J. (2009). *Cognition, evolution, and behavior* (2nd ed.). Oxford, U.K.: Oxford University Press.
Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychological Review, 84*, 127–190.
Shinar, D., Meir, M., & Ben-Shoham, I. (1998). How automatic is manual gear shifting? *Human Factors, 40*, 647–654.
Simon, H. A. (1974). How big is a chunk? *Science, 183*, 482–488.
Simon, H. A., & Chase, W. G. (1973). Skill in chess. *American Scientist, 61*, 394–403.
Somogyi, A. A., Barratt, D. T., & Coller, J. K. (2007). Pharmacogenetics of opioids. *Clinical Pharmacology & Therapeutics, 81*, 429–444.
Spear, E. N., & Riccio, D. C. (1994). *Memory: Phenomena and principles*. Boston, MA: Allyn & Bacon.
Stearns, S. (1992). *The evolution of life histories*. Oxford, U.K.: Oxford University Press.
Stubbe, J. H., & Geus, E. J. (2009). Genetics of exercise behavior. In Y. K. Kim (Ed.), *Handbook of behavior genetics* (pp. 343–358). New York, NY: Springer.
Tanaka, H., & Seals, D. R. (2008). Endurance exercise performance in Masters athletes: Age-associated changes and underlying physiological mechanisms. *Journal of Physiology, 586*, 55–63.
Taylor, P. (1991). Optimal life histories with age dependent tradeoff curves. *Journal of Theoretical Biology, 148*, 33–48.
Telford, C., & Spangler, H. (1935). Training effects in motor skills. *Journal of Experimental Psychology, 18*, 141–147.
Tinbergen, N. (1951). *The study of instinct*. Oxford, U.K.: Oxford University Press.
Tucker, R., & Collins, M. (2012). What makes champions? A review of the relative contribution of genes and training to sporting success. *British Journal of Sports Medicine, 46*, 555–561.

Van de Peer, Y., Maere, S., & Meyer, A. (2009). The evolutionary significance of ancient genome duplications. *Nature Reviews Genetics, 10*, 725–732.

Vatansever, D., Menon, D. K., & Stamatakis, E. A. (2017). Default mode contributions to automated information processing. *Proceedings of the National Academy of Sciences of the United States of America, 114*, 12821–12826.

Vickers, A. J., Bianco, F. J., Gonen, M., Cronin, A. M., Eastham, J. A., Schrag, D., et al. (2008). Effects of pathologic stage on the learning curve for radical prostatectomy: Evidence that recurrence in organ-confined cancer is largely related to inadequate surgical technique. *European Urology, 53*, 960–966.

Walker, R., Hill, K., Kaplan, H., & McMillan, G. (2002). Age-dependency in hunting ability among the Ache of eastern Paraguay. *Journal of Human Evolution, 42*, 639–657.

Ward, A., & Webster, M. (2016). *Sociality: The behaviour of group living animals*. Basel, Switzerland: Springer.

Wennersten, L., & Forsman, A. (2012). Population-level consequences of polymorphism, plasticity and randomized phenotype switching: A review of predictions. *Biological Reviews, 87*, 756–767.

Wooler, R. D., Bradley, J. S., Skira, I. J., & Serventy, D. L. (1990). Reproductive success of short-tailed shearwater *Puffinus tenuirostris* in relation to their age and breeding experience. *Journal of Animal Ecology, 59*, 161–170.

Woollett, K., & Maguire, E. A. (2011). Acquiring 'the knowledge' of London's layout drives structural brain changes. *Current Biology, 21*, 2109–2114.

Wymbs, N. F., Bassett, D. S., Mucha, P. J., Porter, M. A., & Grafton, S. T. (2012). Differential recruitment of the sensorimotor putamen and frontoparietal cortex during motor chunking in humans. *Neuron, 74*, 936–946.

Yarrow, K., Brown, P., & Krakauer, J. W. (2009). Inside the brain of an elite athlete: The neural processes that support high achievement in sports. *Nature Reviews Neuroscience, 10*, 585–596.

Yin, H. H., & Knowlton, B. J. (2006). The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience, 7*, 464–476.

Yoccoz, N. G., Mysterud, A., Langvatn, R., & Stenseth, N. C. (2002). Age– and density–dependent reproductive effort in male red deer. *Proceedings of the Royal Society B: Biological Sciences, 269*, 1523–1528.

Zajonc, R. B. (1965). Social facilitation. *Science, 149*, 269–274.