Wildlife Research, 2022, 49, 89–99 https://doi.org/10.1071/WR20105

Supplemental feeding of northern bobwhite (*Colinus virginianus*) and dietary requirements: a review

Brett J. Henry^{A,*}, Matthew Z. Brym^{A,*}, Cassandra Henry^{A,*} and Ronald J. Kendall $^{\bigcirc}$ A,B

Abstract. Northern bobwhites (*Colinus virginianus*) are a well known game bird that has been extensively studied and managed throughout its range for many decades. Despite this, bobwhites have continued a steady annual decline across the United States, irrespective of many well established conservation practices in place to mitigate this. Supplemental feeding is one such technique that is a widely used tool in bobwhite management, but the methods and results of the studies to investigate the effectiveness of this method are highly variable. The effectiveness of supplemental feeding practices is further hindered by the limited knowledge regarding the nutritional requirements of wild bobwhite because many of the guidelines that researchers follow are based on species of Galliformes that are primarily used for production. Here, we review supplemental feeding studies, nutritional requirements of bobwhite, and discuss future directions.

Keywords: bobwhite, Colinus virginianus, management practices, nutrition, supplemental feed.

Received 24 November 2020, accepted 18 June 2021, published online 15 October 2021

Introduction

North American grassland birds overall have declined by 53% since 1970, but northern bobwhite (Colinus virginianus; hereafter bobwhite) populations have declined by 78% in that time (NABCI 2019). Although bobwhite population declines have been noted for over a century (Nice 1910; Stoddard 1931), it was Brennan's (1991) article noting 'alarming' declines that spurred a nationwide conservation effort for the bobwhite (Hernández et al. 2013). Despite these efforts, the bobwhite topped the Audubon's list of the top 10 common birds in decline in 2007 (Butcher 2007), and bobwhites continue to decline at a rate of 3.5% per year as of 2015, which is a higher rate than 94% of all other declining birds (Sauer et al. 2017). The declining numbers resulted in 27 states listing the bobwhite as a species of greatest conservation need in their State Wildlife Action Plans (SWAP), and only 19 of the 865 birds reported are listed on more SWAPs (USGS 2020).

To compound this further, hunters have been integral to bobwhite conservation initiatives by contributing millions of dollars (Brennan 2015); however, hunter participation is decreasing with the decline of the bobwhite (Burger *et al.* 1999), potentially hindering funding for bobwhite conservation. Purvis (2011) reported that quail hunting had seen a 79% decrease by 2010 in Texas alone, a state considered to have

the last strongholds of bobwhite (Brennan *et al.* 2007). With such an extreme decrease in participation, state agencies are less likely to allocate funds towards quail (Rollins 2002), and rural communities will experience negative economic impacts (Burger *et al.* 1999; Johnson *et al.* 2012).

There are many questions concerning the decline because bobwhites are considered to be one of the best studied wildlife species, and management practices for bobwhite are well documented and understood (Guthery 1997; Williams *et al.* 2004; Hernández *et al.* 2013). Despite the concern for dwindling bobwhite numbers and economic impacts, conservation initiatives have been unsuccessful at reversing the decline (Hernández *et al.* 2013). This, in part, could be due to management practices that have remained static for decades (Williams *et al.* 2004; Stribling and Sisson 2009). Oftentimes, the foundation for these management practices is based on studies that were conducted over 50 years ago (e.g. Stoddard 1931; Leopold 1933; Edminster 1954; Rosene 1969), and these studies are still being cited even in management books that have been published within the past 15 years (Brennan 2007; Hernández and Guthery 2012).

Williams *et al.* (2004) and Guthery (2002) both expressed concern for the lack of change in management practices and called for adaptations to the 'historical management'; thus, it is necessary to periodically re-evaluate management practices. One

^AThe Wildlife Toxicology Laboratory, Texas Tech University, PO Box 43290, Lubbock, Texas 79409-3290, USA.

^BCorresponding author. Email: ron.kendall@ttu.edu

^{*}These authors contributed equally to this work.

Wildlife Research

B. J. Henry et al.

such management practice that should be evaluated is supplemental feeding. This practice has been shrouded in contradictory results, yet is still widely used to this day. Here, we will summarise the research conducted on supplemental feeding, the nutrition of bobwhite, and propose future considerations.

Supplemental feeding

90

Supplemental feeding of game species is a common management technique that has been popular with land managers and wildlife enthusiast for many decades. The simplicity and seemingly logical benefits of supplemental feeding have contributed to the practice being widely used for quail, although, to our knowledge, there were few, if any, formal investigations into the effectiveness of supplemental feeding as a management tool for bobwhite until the late 1940s (Frye 1954). Since then, numerous studies have investigated a variety of supplemental feeding strategies and their effects on bobwhite (Table 1). Here, we provide a broad overview of this work and highlight where further research may improve our understanding of the topic.

Food plots

Food plots are typically implemented as a means of supplementing seasonal shortages of food, so as to increase the survivability of game. For bobwhite, winter is a period of scarcity and land managers frequently attempt to increase overwinter survival with plantings of milo, soybeans, corn, wheat and/or legumes (Rollins 2007; Hernández and Guthery 2012). Robel (1969) illustrated the potential of food plots to offset limited food resources, because higher weight and body fat were documented in bobwhite that overwintered in the vicinity of food plots. Additional studies produced similar results, suggesting that food plots may improve the survival of bobwhite under adverse winter conditions (Robel 1972; Robel et al. 1974). However, despite the apparent benefits of food plots to the condition of bobwhite, Robel (1969) acknowledged that understating the effects of this practice on the survivability of wild bobwhite required further study. This remains a challenge for researchers to this day, because the effects of food plots may be confounded by environmental conditions and resource availability.

For example, the increases in bobwhite weight and fat content documented in early studies were present only during 2-3 months between winter and spring, with bobwhite making heavy use of native forage outside of this period (Robel 1969, 1972; Robel et al. 1974). Overwinter mortality of bobwhite both near to and far from food plots was also found to be similar during mild winters (Robel and Kemp 1997), and radiotelemetry studies documented no differences in the homerange sizes and movement of bobwhite between sites with and without food plots (Madison et al. 2000). Because increased movement and larger home ranges are typically indicative of poor-quality bobwhite habitat (Singh et al. 2011), we would expect to see less movement and smaller home ranges in areas with food plots if these were having a positive effect on habitat quality. Consequently, the similarity in home-range sizes documented by Madison et al. (2000) suggests that food plots did not improve habitat in their respective areas, although these authors suspected that their findings may have been influenced by mild winters during their study. Indeed, Robel and Kemp (1997)

observed that food plots tended to have a proportionally higher mitigating effect on bobwhite mortality as the severity of environmental constraints increased. Madison *et al.* (2000) therefore concluded that the potential benefits of food plots may be contingent on environmental conditions, with the greatest benefit occurring during periods of inclement weather and scarce resources. A study of bobwhite home ranges in Florida corroborates this inference, as the presence of food plots reduced the size of bobwhite home ranges when food was limiting during the winter, but not during the summer (Singh *et al.* 2011).

Although the aforementioned studies have illustrated that the potential benefits of food plots are largely dependent on environmental conditions, additional effects associated with the practice have been documented. For instance, a study in east Texas during the breeding period reported that juvenile bobwhites selected food plots over native habitat because of the increased presence of arthropods, which are an important protein source for quail chicks (Parsons et al. 2000; Hernández and Guthery 2012). Although this is an unintended consequence of food plots, it highlights the possibility of food plots serving as brood habitat for bobwhite. Conversely, Peoples et al. (1994a) found that food plots may lead to deficiencies in crude proteins and essential amino acids, because quail fed on supplemental grain during the summer instead of foraging for insects. Another unintended consequence of food plots may be to increase densities of both avian and mammalian predators of quail, which may increase susceptibility of bobwhite to predators (Godbois et al. 2004; Turner et al. 2008). A similar hypothesis has also been proposed regarding the potential of food plots to concentrate bobwhites, making them more susceptible to hunting pressure; however, research into the topic has proven inconclusive thus far (Madison et al. 2002).

In summary, food plots were the most frequently researched supplemental feeding strategy for bobwhite, with there being 14 studies on this topic. However, six studies were conducted on the Fort Riley Military Reservation in Kansas and four of these occurred during overlapping years (Table 1). Two other food plot studies took place on the Babcock-Webb Wildlife Management Area in Florida, with both encompassing the same time period as well (Table 1). The inferences drawn from these studies should therefore be interpreted cautiously because they may not be entirely representative of the effects of food plots on bobwhite, which occupies a wide geographical distribution and experiences dramatic population fluctuations among years (Hernández and Peterson 2007; Sauer et al. 2017). This is exacerbated because the potential benefits of food plots are contingent on environmental conditions and resource availability, which vary among regions. These confounding variables may explain why some studies found advantages to food plots, whereas others documented no difference (Table 1) or lower bobwhite populations than regional norms (Ellis et al. 1969). Consequently, although food plots may be a valuable tool for bobwhite management, it is important to also consider the impacts of other factors, such as environmental conditions and habitat quality, when using them.

Stationary feeders

Another supplementary feeding technique often employed in bobwhite management is the use of stationary feeders. These

Table 1. Summary of supplemental feeding studies in order of year Asterisk (*) indicates thesis or dissertation. N/A, not applicable

Study year(s)	Location	Supplemental feeding type	Frequency and duration of feed	Effect evaluated	Results	Source
1948–1953	Florida	Gravity feeders with	Bi-weekly; year-round	Density	Increased density in feeder areas	Frye 1954
1952–1954	Alabama	Gravity feeder with cracked corn or turkey feed	Bi-weekly or as needed; year-round	Feeder use; density	Quail received 5% of the food Density did not increase	Haugen 1957
1954–1955	Kentucky	Gravity feeder with scratch feed	Year-round	Feeder use; density	Quail received ~1% of the food Did not increase nonulations	Collins 1956
1961–1967	Kansas	Food plots	N/A	Diet; weight; body fat	Volume in crop did not differ Increased weight in 2 of 4 months Increased hothy far in 2 of 4 months	Robel 1969
1961–1972	Kansas	Food plots	N/A	Diet; weight; body fat	Diet affected only Jan.—2 or + months Diet affected only Jan.—Apr. Increased weight in 3 of 8 months Increased holy far in 3 of 7 months	Robel <i>et al.</i> 1974
1961–1980	Kansas	Food plots	N/A	Winter mortality	Lower mortality of an arrow of the Lower mortality of mortality of mortality of mortality	Robel and Kemp 1997
1963–1965 1968–1972 1975–1981	Illinois Kansas Wisconsin	Food plots Food plots Food plots	N/A N/A 1976–1977 grain added	Density Body fat; weight Density	Decreased density Weight and body fat differed only Jan.—Mar., not Sep.—Dec. 1 year had increased populations compared with range-wide	Ellis <i>et al.</i> 1969 Robel 1972 Dumke 1982
1985–1987	Texas	Drum/bucket feeders with milo	2× weekly; late fall–Mar.	Winter survival; reproduction	No difference in reproduction Only deep sand sites had increased survival	Doerr and Silvy 2002
1986–1987	Texas	Bucket feeders with milo	2× weekly; Nov–Mar	Body fat; fall density	Body fat increased Fall densities did not increase	Doerr and Silvy 2006
1989–1990	Oklahoma	Food plot/gravity feeder	N/A	Diet; weight; body fat; nutrients	Differences in dietary protein quality No effect on weight or body fat Deficient in ≥ I amino acid	Peoples et al. 1994a
1991–1996 1991–1996	Oklahoma Oklahoma	Gravity feeder with milo Gravity feeder with milo	Ad libitum; year-round Ad libitum; year-round	Density; covey size Mortality	No difference in covey size or density Increased mammalian predation and hunting mortality near feeders	DeMaso et al. 2002 DeMaso et al. 1998
1991–1992 1992–1996	Texas Oklahoma	Food plots Barrel feeders with milo	N/A N/A	Juvenile use Winter survival	Food plots used more than native vegetation Increased survival for 2 years I year control had increased survival	Parsons et al. 2000 Townsend et al. 1999
1993–1996	Georgia	Roadside with milo and whole corn	Bi-weekly; Nov.–May	Home-range size; survival	Decreased home-range size Increased survival first year No difference 2nd year	Sisson et al. 2000
1994–1997	Kansas	Food plots	N/A	Movement; home-range size	2 of 3 years no difference in daily movement No difference in home-range size	Madison et al. 2000
1994–1997	Kansas	Food plots	N/A	Hunting; survival	Hunter mortality was inconsistent Survival effect inconclusive	Madison et al. 2002
2000–2001	Georgia	Food plots and feed trails with milo	Nov.–May	Response of predators	Bobcats found closer to supplemental food than expected	Godbois et al. 2004

(Continued)

Table 1. (Continued)

Study year(s)	Location	Supplemental feeding type	Frequency and duration of feed	Effect evaluated	Results	Source
2000–2003	Texas	Gravity feeders and	As needed; 2× weekly	Home-range size; survival	Decreased home-range size	Guthery et al. 2004
		roadside with grains	Oct.–Mar.	`)	No effect on survival	
2000–2003	Texas	Gravity feeders and roadside with grains	As needed; 2× weekly Oct.—Mar.	Body mass	Increased mass Sep.–Mar.	Hiller and Guthery 2004
2001-2003	Texas	Roadside with milo and	; NovDec.	Home-range size; survival	Home-range size; survival Home-range size smaller and survival lower than control	Haines et al. 2004
		corn			1st year No difference 2nd year	
2001–2007	Florida	Feed trail with milo	Every 2 weeks; year-round	Home-range size; habitat selection	Home-range size was reduced during breeding season Preference for feed trail	Wellendorf et al. 2017
2002-2003	Texas	Barrel feeders with milo	As needed; year-round	Feeder use	Raccoons accounted for the most feeder visits	Henson et al. 2012
2002-2003	Florida	Feed trail with milo	Bi-weekly; year-round	Winter diet; body mass	Milo accounted for 67.5% of diet	Whitelaw et al. 2009
	Georgia				Body mass increased	
2002-2007	Florida	Food plots	N/A	Home-range size	Decreased home-range size	Singh et al. 2011
2002-2008	Florida	Food plots	N/A	Reproduction	Did not affect reproduction	Rolland et al. 2011
2004-2005	Georgia	Food plots and feed trails	Every 2–6 weeks;	Response of predators	Red-tailed hawks found closer to supplemental food than	Turner et al. 2008
		with milo	OctMay		expected	
2008	Texas	Roadside with 2 types of rations	Weekly; year-round	Nesting; density	Protein—carbohydrate (PC) and carbohydrate only (CO) ration had no difference in nesting or density	Tri et al. 2012
2008	Texas	Roadside with corn and	Weekly; year-round	Home-range size	No control	Tri et al. 2014
		milo or protein feed			No difference in home-range size	
2009	Georgia	Feed trail with cereal grains	2× per month; Oct.—June	Non-target species use	Non-target species utilised food most	Morris et al. 2010
2009–2010	Florida	Feed trail with milo	Bi-weekly; year-round	Dispersion; home-range size; diet	Less daily dispersion No difference in home-range size	Miller 2011*
2010-2012	Texas	Broadcast milo into	$2\times$ per month; year-round Home-range size; survival		I otal body lipids differed No effect on female home range	Buckley et al. 2015
		vegetation			Increased survival	
2011–2012	Texas	Broadcast milo into	$2 \times$ per month; year-round	Reproduction	Increased nest attempts No difference for nest success, clutch size, or eag volume.	Buckley et al. 2018
2013-2015	Texas	Broadcast milo into	$2 \times$ per month; year-round	Survival	Increased winter survival	McLaughlin et al. 2019
2013_2015	Tevas	vegetation Broadcast milo into	2> ner month vest round Remoduction	Reproduction	Outsh size increased for I was	Wilew 2017*
	COVE	vegetation	Z Per monan, year roans		No difference in egg volume, brood success, nest attempts	
2013–2015	Georgia	Feed trail with milo	Every 2 weeks; DecMar. Habitat selection and May-Oct.	Habitat selection	Feed trail selection stronger in winter Brooding birds selected habitat near feed trail	McGrath et al. 2017

range from simple barrels and drums, to specifically designed automated feeders that can distribute a variety of feed, with corn, poultry feed and milo being common options. Like food plots, stationary feeders are intended to help offset shortages of food, although they are easier to use and may be utilised in areas where environmental conditions and land use impede the establishment of the former (Frye 1954).

A pioneering study by Frye (1954) reported substantial increases, averaging as high as 179.80%, in quail abundance in areas where stationary feeders were deployed. This led Frye (1954) to conclude that supplemental feeding via stationary feeders presented a practical means of increasing quail abundance in areas with limited food availability. However, since then, research into stationary feeders has produced evidence that the effects of this management practice on bobwhite may be more abstruse than initially reported. For example, studies have documented increases in weight and body fat of bobwhite overwintering in areas with stationary feeders (Hiller and Guthery 2004; Doerr and Silvy 2006), which were similar to the results obtained with food plots (Robel 1972; Robel et al. 1974). However, the stationary feeders did not improve survival or abundance. Doerr and Silvy (2006) postulated that this was because the milo provided did not supply the nutrients required by bobwhite for breeding, thus limiting the potential for population growth following supplemental feeding. Additionally, Doerr and Silvy (2006) stressed that food supply was only one of many compounding factors that must be considered when developing and implementing supplemental feeding, if an effective outcome is to be achieved.

An example of one such factor that may hinder potentially beneficial effects of stationary feeders is competition with nontarget species because it has been documented that quail received <5% of the feed provided (Collins 1956; Haugen 1957). Since then, more studies have confirmed this possibility, with bobwhite accounting for only 7.3% of visits to stationary feeders (Henson et al. 2012). Additionally, it has been purported that stationary feeders may increase the susceptibility of bobwhite to hunters and predators by causing quail to become concentrated (Madison et al. 2002). Although higher rates of mortality owing to hunting and mammalian predators were documented in the vicinity of feeders, there was no effect on average annual bobwhite mortality, and supplemental feeding merely shifted the distribution of mortalities (DeMaso et al. 1998). This was corroborated by Guthery et al. (2004) who also found that mortality was unaffected by supplemental feeding, despite the practice resulting in more localised distributions of quail.

Overall, studies into supplemental feeding of bobwhite with stationary feeders have produced results similar to those that investigated the effects of food plots. Some found the potential of stationary feeders to increase quail survival and densities in areas with limited food resources (Townsend et al. 1999; Doerr and Silvy 2002), whereas others documented supplementation with stationary feeders to be a neutral management practice (Guthery et al. 2004). Once again, there was a general consensus that stressed the importance of considering multiple variables and using supplemental feeding as part of a larger management strategy. In particular, management practices that resulted in quality habitat and food resources that were sufficient to not only survive overwintering, but also meet other essential nutritional

requirements of bobwhite, were emphasised (DeMaso *et al.* 1998, 2002; Doerr and Silvy 2002).

Broadcasting, feed trails, and roadside feeding

The final supplemental feeding strategy commonly used in bobwhite management entails periodically distributing feed, often milo, into the environment. Although the distribution methods for broadcasting, feed trails and roadside feeding are different, we will hereafter refer to all of these as broadcasting for ease of discussion. Studies into the effects of broadcasting yielded results similar to those of other supplemental feeding strategies, with a degree of variability being present. Reductions in home-range sizes of bobwhite in areas with broadcasting have been reported by some (Sisson et al. 2000; Haines et al. 2004), whereas others have found no differences between areas with and those without broadcasting (Miller 2011; Tri et al. 2014; Buckley et al. 2015). Research into the effects of broadcasting on survival of bobwhite has likewise produced varying results. For example, Sisson et al. (2000) reported increased survival of bobwhite where broadcasting was employed during the first year of a 2-year study, whereas the 2-year study of Haines et al. (2004) documented the opposite. However, other studies have consistently documented increased survival rates associated with broadcasting, which was attributed to the practice being effective at offsetting food scarcity (Buckley et al. 2015; McLaughlin et al. 2019). This is consistent with research that determined stationary feeders and food plots had more pronounced benefits in poor quality habitat and during periods of duress (Robel and Kemp 1997; Doerr and Silvy 2006).

Additionally, more contemporary studies of broadcasting have begun to investigate the effects of this practice on bobwhite reproductive success and nutrition. For instance, McGrath et al. (2017) reported bobwhite preferentially selects habitat in the vicinity of feed trails during both the winter and breeding period, which could positively affect bobwhite reproduction. Wiley (2017) and Buckley et al. (2018) affirmed this potential, because they found that bobwhite supplemented with broadcasting had larger clutch sizes and made more nesting attempts respectively. Despite these promising findings, the overall impact of broadcasting on breeding success was unclear, because no differences were observed in nest success, egg volume or brood success. This may be due to the authors' use of grain for broadcasting, which is often deficient in nutrients essential for breeding quail (National Research Council 1994; Sauvant et al. 2004); however, Tri et al. (2012) found that using a protein carbohydrate or carbohydrate only ration made no differences in bobwhite nesting and density. However, further study is needed to assess the impacts of supplemental feeding with nutrient-fortified rations on bobwhite, because, to our knowledge, only a very limited number of studies have assessed the nutritional requirements of wild quail, and those that do exist, provide only a cursory examination of the topic.

Summary

Supplemental feed studies have yielded promising results about the potential of this management technique to serve as a tool for bobwhite management. However, more research into supplemental feeding is needed to better understand how other factors Wildlife Research
B. J. Henry et al.

may influence the effectiveness of this practice and how it may vary among regions. Additional research into the potential effects of nutrient fortified feed would also be valuable, because many commonly used supplementary feeds may not fully meet the nutritional requirements of bobwhite (Peoples *et al.* 1994*a*; Doerr and Silvy 2006). Consideration of the nutritional requirements of bobwhite and research into supplemental feeding strategies that incorporates this insight may therefore yield a more complete understanding of supplemental feeding as a tool for bobwhite management, as well as more effective supplemental feeding practices in the future.

Nutrition

94

Early studies to elucidate the dietary requirements of bobwhite focussed primarily on protein, calcium, phosphorus and vitamin A (Nestler 1949). These studies were successful in determining the appropriate proportions of feed materials to be used for growth, breeding and livability of pen-raised bobwhite, which were compiled for use as recommendations for bobwhite rearing in 'Nutrition of Bobwhite' (Nestler 1949). Later, the National Research Council published a revised version in 'Nutrient Requirements of Poultry' in 1994 based on the available research. Direct guidelines are given for the nutrients that should be available in the diets of pen-raised bobwhite, including levels of protein, methionine, cystine, calcium, phosphorus, vitamin A, riboflavin, pantothenic acid, niacin and choline (National Research Council 1994). These guidelines, even though published in 1994, remain a primary source of dietary requirements for pen-raised bobwhite. The amount of information known specifically for the bobwhite is significantly less than for other species, such as the Japanese quail (Coturnix japonica; National Research Council 1994). Additionally, because bobwhites are a species of Galliformes, it is generally accepted that it is susceptible to similar nutritional diseases as are other prominent Galliformes species, such as chicken or turkey (Barnes 1987). Below we present the available information on bobwhite nutrition, which can help guide supplemental feeding practices.

Protein and amino acids

Many early studies focussed on discerning the required percentage of dietary protein for optimal growth and reproduction capabilities of captive bobwhite, with a progressive decrease in total protein required when appropriately supplemented with specific amino acids. Initially, Norris (1935) found that a diet comprising 27% crude protein was the best for growth up to 8 weeks. Shortly after, studies found that a diet of 28% crude protein was optimal for survival during the first 10 weeks of life (Nestler et al. 1942; Baldini et al. 1950; Andrews et al. 1973). However, Baldini and Zarrow (1952) noted that these levels of crude protein were high compared with other white egg layers, and this may have resulted from a deficiency in other essential nutrients. The studies previously mentioned utilised feeds that were formulated of soybean meal or ground corn, which are notoriously low in two essential amino acids, methionine and lysine (Klasing and Korver 2019). Later, studies demonstrated that 20-26% crude protein rations formulated of soybean meal and ground corn when supplemented with the appropriate essential amino acids were sufficient for raising bobwhite

(Baldini *et al.* 1953; Scott *et al.* 1963; Serafin 1982; Aboul-Ela *et al.* 1992; Blake and Hess 2013). Additionally, Serafin (1977, 1982) found that a diet with 24–26% protein supplemented with 1.0% methionine and cystine, both being sulfur-containing amino acids, improved growth of bobwhite compared with an unsupplemented 32% protein diet. This is likely to have resulted because sulfur-containing amino acids are thought to be a major limiting factor of bobwhite (Peoples *et al.* 1994*b*).

However, wild bobwhites have access to many natural foods that supply them with the necessary nutrients and essential amino acids (Wood et al. 1986; Peoples et al. 1994b; Boren et al. 1995). For example, bobwhites consume more seeds to meet its energy expenditure needs during the winter months when sources of protein, such as insects, are much scarcer (Rollins 2007; Hernández and Guthery 2012). In fact, the bobwhite dietary requirements not only vary depending on time of year but also throughout the life cycle. Although the dietary protein requirement for overwintering bobwhite is only 12% (Nestler et al. 1944a), protein requirements are more than double that during growth periods (Harveson et al. 2004; Rollins 2007), and a diet comprising 23% protein is recommended for breeding wild bobwhite females (Nestler et al. 1944b; Hernández and Guthery 2012). These requirements are typically met by increased invertebrate consumption by bobwhite chicks and breeding females. This was confirmed further by Peoples et al. (1994a) through crop analysis, which corroborated the increased invertebrate content in the crop of bobwhite during the summer breeding season and a lower protein content during the winter.

The amount of protein required by Galliformes and bobwhite are in part to satisfy the need for the 10 essential amino acids that cannot be synthesised, and deficiency in these amino acids can result in decreased growth in chicks and/or reduction in bodyweight, whereas breeding females have decreased egg production or egg size (Klasing and Korver 2019). There are also upper limits to dietary protein, because overabundance of protein can result in the increase in uric acid production, which can lead to gout, and specific amino acids in excess concentrations can result in amino acid toxicity (Klasing and Korver 2019).

Calcium and phosphorus

Calcium and phosphorus are particularly important for bone formation (Klasing and Korver 2019), with the skeleton holding ~99% and 80% of the calcium and phosphorus respectively (Nestler *et al.* 1948). Calcium is also vital to many other functions such as cellular signalling, blood clotting and muscle contraction (Klasing and Korver 2019). The amount of calcium required for bobwhite varies among life stages. The earliest report indicated that 0.75% phosphorus and 1.00% calcium would be optimum for bobwhite chicks (Nestler *et al.* 1948). However, it was reported later that growth of bobwhite chicks from 0 to 6 weeks of age on a ration containing a 1:1 ratio of calcium to phosphorus at 0.65% of the diet each was found to be optimal (Wilson *et al.* 1972), which is in close agreement with the 0.6% phosphorus requirement reported by Scott *et al.* (1958).

Furthermore, breeding bobwhite, particularly females, have been shown to require higher concentrations of phosphate and much higher concentrations of dietary calcium for eggshell production (DeWitt *et al.* 1949; Cain *et al.* 1982). DeWitt *et al.* (1949) reported that 2.3% dietary calcium and 0.80%

phosphorus resulted in the optimal breeding capacity of adult female bobwhite. The later study by Cain *et al.* (1982) confirmed this metric with a similar result of 2.4% dietary calcium and >0.70% phosphorus for breeding bobwhite. Furthermore, decreases in dietary calcium for breeding bobwhite hens result in lower egg production as well as the mobilisation of calcium from bones to facilitate egg production (DeWitt *et al.* 1949; Cain *et al.* 1982; Klasing and Korver 2019). However, these numbers are for facilitation of captive breeders producing up to 100 eggs a year, and a wild bobwhite may be able to produce a clutch of 12–15 eggs with significantly lower requirements by mobilising the required nutrients from the body (Cain *et al.* 1982).

Excess calcium or phosphorus taken in through the diet can usually be excreted without issue, and limited deficiency can be mitigated by decreased excretion (Nestler *et al.* 1948). However, extremely high concentrations of either calcium or phosphorus will cause a deficiency in the opposing mineral. Deficiency in phosphorus can induce rickets in Galliformes, as well as interfere with the uptake of other essential minerals (Klasing and Korver 2019). Additionally, excess phosphorus is known to cause eggshell thinning by causing calcium deficiency (Klasing and Korver 2019). This outlines how important it is to properly balance these essential minerals in feed material.

Vitamins

Vitamin are essential in the diets of all organisms and bobwhite is no exception. Vitamins have a multitude of functions including enzymatic cofactors, antioxidants and formation of hormones (Klasing and Korver 2019). Many of these compounds, much like essential amino acids, either cannot be synthesised or cannot be synthesised in necessary quantities to facilitate function. Additionally, deficiency in vitamins can be more detrimental to health and survivability than deficiency in other nutrients (Klasing and Korver 2019).

The National Research Council (1994) only lists vitamin requirements for vitamin A, riboflavin, pantothenic acid, niacin and choline. Choline, although not a vitamin, is an essential nutrient that has been studied and typically included in dietary supplementation. Of the above vitamins and nutrients, only vitamin A has a listed value for adult bobwhite (8800 IU kg⁻¹), with the remainder being listed for bobwhite between 0 and 10 weeks old (13 200 IU kg⁻¹). These data are from studies by Nestler (1946), in which he found that deficiency of vitamin A has negative consequences for reproduction and survival of adults, as well as survival of offspring. Additionally, an assessment of bobwhite fed a vitamin A-deficient diet resulted in bobwhite developing visceral gout (Nestler and Bailey 1943). Conversely, some excess vitamin A can be stored in fatty tissue or the liver, but in cases with improper feed mixing that results in extremely high levels of vitamin A, hypervitaminosis can occur and has many negative consequences (Klasing and Korver 2019).

Additionally, these studies on captive bobwhite were followed by studies with wild bobwhite (Schultz 1948; Lehmann 1953). Schultz (1948) did not find evidence that vitamin A affected bobwhite populations in Ohio, but Lehmann (1953) believed that vitamin A deficiencies facilitated heavier parasite burdens and affected winter survival in south Texas. However,

both noted that vitamin A was variable not only among different sites but within coveys. Considering the limited and contradictory evidence for vitamin A, more research should be conducted to evaluate the vitamin A requirements needed by wild bobwhite because deficiencies in vitamin A have led to a compromised immune system in chickens (Dalloul *et al.* 2002).

Studies regarding the other vitamins are even more limited than those for vitamin A, with there being only two studies. Serafin (1974) undertook several experiments to assess the effects of various concentrations of riboflavin, niacin, pantothenic acid and choline. Growth was found to be inhibited, and mortality occurred by 5 weeks in bobwhite whose diet was deficient in the listed B vitamins. The studies found that the quantities required of each are ~ 3.8 , ≤ 31.0 , 12.6 and 1500 mg kg⁻¹ for riboflavin, niacin, pantothenic acid and choline respectively (Serafin 1974). A similar amount of pantothenic acid was previously reported by Scott *et al.* (1964). There are several ailments that are associated with deficiencies in each of these vitamins for Galliformes (see Swayne 2019).

Summary

This is, to our knowledge, the current nutritional information available that has been conducted specifically for bobwhite. However, there are many other specific amino acids, vitamins, minerals and essential nutrients that could be studied to give a more complete picture of the necessary dietary levels for bobwhite and their function. The importance of a balanced diet for captive bobwhite has been thoroughly studied for the above nutrients, and it is equally important that wild bobwhite has balanced feed for supplementation.

Conclusions

As discussed, supplemental feeding is a widespread and longrunning practice for bobwhite management that many believe to be beneficial, but these benefits may be contingent on a variety of factors. The studies discussed here have illustrated this contextual dependence, with some finding that supplemental feeding had no effect on bobwhite, whereas others have documented positive impacts on survival and fecundity. This variability in results may occur because of the variety of methods employed, as well as the pressures that individual bobwhite populations face, such as harsh winters and periods of drought. Thus, there is a need to consider what supplemental feeding may accomplish, during what times it is most effective, and what kind of feed to use.

For example, Peoples *et al.* (1994*b*) suspected that supplemental feeding of bobwhite may cause birds to replace portions of what would be an insect-rich diet with supplemental grain. In the study by Peoples *et al.* (1994*b*), grain was provided during the entire year and bobwhite collected form areas with supplemental feed exhibited decreased consumption of insects and a subsequent deficiency in crude protein and essential amino acids during the breeding period when compared with those from untreated areas. Other studies have corroborated this possibility, because they have shown that bobwhite is capable of increasing the amount of food consumed when fed a ration that is purposefully below its energy requirements but would not compensate for a protein deficit in the same manner (Giuliano *et al.* 1996). It is therefore possible that supplemental feeding during the

Wildlife Research

B. J. Henry et al.

summer breeding season, especially with low protein grains, can negatively affect the breeding fitness of wild bobwhite.

96

More specifically, current supplemental feeding practices rely predominantly on milo (Table 1), which may not provide the complete nutritional requirements of bobwhite throughout the year. Milo is a high-energy ration, 3800 kcal kg⁻¹ (Sauvant et al. 2004), that meets the energy requirements of bobwhite, 2850– 3170 kcal kg⁻¹ (Wilson et al. 1977); thus, milo is suitable to facilitate the survival of adult bobwhite through the winter, (Hernández and Guthery 2012; Brown and Hayslette 2019), which has been demonstrated in supplemental feeding studies (Table 1). However, milo contains, on average, only 9.5% crude protein, 0.3% calcium and 0.3% phosphorus (Sauvant et al. 2004; Hernández and Guthery 2012). These numbers are well below those required to optimise reproduction of female bobwhite, and milo may also be deficient in other key nutrients. Therefore, supplemental feeding with energy rich rations to offset dietary stress in the winter and then switching to a higher protein ration during the following spring may facilitate a stronger reproductive potential in bobwhite during the breeding season.

Furthermore, proper nutrition is not only important to increase breeding capacity, but also to ensure the overall health and immune system function. Nutritional deficiencies in nutrients, such as amino acids, minerals and vitamins, can have suppressive effects on the avian immune system (Cook 1991). Additionally, the diet has regulatory effects on many functions of the body including the immune system (Kogut and Klasing 2009), and studies have shown that proper nutrition has the potential to minimise the impact of infectious diseases by enhancing the immune system in poultry (Klasing 2007). In contrast, an impaired immune system can lead to decreased growth, decreased production, and increased mortality when birds are plagued with infectious diseases, whether they be viral, bacterial and/or parasitic (Humphrey and Klasing 2004; Klasing 2007). The immune system also often competes with growth or reproductive processes for nutrient allocation, and immune responses have the capacity to alter bodily functions such as metabolism and digestion if necessary (Koutsos and Klasing 2001). Optimisation of the immune response is dependent on many factors, and the immune system takes priority in the distribution of nutrients during times of infections. This is particularly important as wild bobwhite is exposed to numerous stressors, such as nutrient deficiency, chemical exposure, and parasitic infections, that are known to adversely affect the avian immune system (Kogut and Klasing 2009). Consequently, further research into nutrition, supplemental feeding, and the interactions of these variables on wild bobwhite is necessary.

However, it should be noted that the information available specifically for bobwhite dietary requirements is limited, and the majority of these studies was focussed mainly on macronutrients, vitamin A and vitamin B for the optimal growth to breed and raise captive bobwhite. This scarcity of information into the specific nutritional requirements of bobwhite can be partially offset by referencing the requirements of other closely related species of Galliformes, such as the Japanese quail or chicken, because these have been extensively studied and are well documented. However, although the nutritional requirements of these birds are expected to be similar, there is likely to be

some variation because there are differences among the species. This variation must be considered when making assumptions into the nutritional requirements of bobwhite that are derived from information documented for other species of Galliformes. There is also likely to be more variation between the nutrient requirements of a pen-raised bird versus a wild bird, which should be considered as well. Nevertheless, this information can still be utilised to assist the resurgence of wild bobwhite if employed cautiously.

Unfortunately, the lack of information regarding wild bobwhite nutrient requirements and high variation in results prevents specific recommendations on type of feed, supplemental feeding type, or when supplemental feeding is needed; however, some recommendations can be made on the basis of the provided literature. It is imperative that any supplemental feeding be approached with bobwhite nutrition in mind, and future study designs that incorporate a variety of supplemental feeds with different nutritional values could provide more insight into the nutrient requirements of wild bobwhite. Nevertheless, it is well documented that bobwhite females and juveniles require a highprotein diet during the breeding season. A feed that is supplied during this time should meet this requirement because bobwhite may replace part of their natural diet, such as insects, with the supplemental feed (Peoples et al. 1994b). In contrast, a highenergy ration provided in the winter could enhance the survival of bobwhite. There is also a great need to compare the supplemental feeding methods at the same site and across regions because the variation in habitat type, for example, can influence the efficacy of the method.

Fortunately, continued research has gradually improved our understanding of bobwhite and the myriad factors that influence their populations, as well as how these same factors may affect the management practices that seek to protect them. Although traditional management practices, such as supplemental feeding, have produced inconsistent results, studies have demonstrated that using these methods during the appropriate times and circumstances may have substantial benefits. For instance, supplemental feeding during times of stress, particularly in winter and drought, gives the individual bobwhite a greater chance of overcoming these stressors and may improve the overall survivability of populations. The benefits of supplemental feeding may be further bolstered if we consider the seasonal and life-stage nutritional requirements of wild bobwhite, because this would allow the provision of fortified rations to fulfill key nutritional requirements of breeding females, thereby improving breeding potential. To that end, future studies into supplemental feeding should also consider factors such as nutrition, habitat quality and climatic variables. Research that integrates these points into supplemental feeding strategies may leave land managers with a greatly improved set of tools to manage their quail.

Data availability statement

Data sharing is not applicable as no new data were generated or analysed during this study.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

We also express our gratitude to Park Cities Quail Coalition and the Rolling Plains Quail Research Foundation for their patronage and support of our quail research.

Acknowledgements

We thank all the land managers, researchers and wildlife enthusiasts for the countless hours of work they have put in to better understand and protect northern bobwhite quail. The contributions of these individuals have amounted to decades of labour and enabled the conservation one of North America's most iconic game birds.

References

- Aboul-Ela, S., Wilson, H. R., and Harms, R. H. (1992). The effects of dietary protein level on the reproductive performance of bobwhite hens. *Poultry Science* 71, 1196–1200. doi:10.3382/ps.0711196
- Andrews, T. L., Harms, R. H., and Wilson, H. R. (1973). Protein requirement of the bobwhite chick. *Poultry Science* 52, 2199–2201. doi:10.3382/ps. 0522199
- Baldini, J. T., and Zarrow, M. X. (1952). Estrogen and serum calcium levels in the bobwhite quail. *Poultry Science* 31, 800–804. doi:10.3382/ps. 0310800
- Baldini, J. T., Roberts, R. E., and Kirkpatrick, C. M. (1950). A study of the protein requirements of bobwhite quail reared in confinement in battery brooders to eight weeks of age. *Poultry Science* 29, 161–166. doi:10.3382/ps.0290161
- Baldini, J. T., Roberts, R. E., and Kirkpatrick, C. M. (1953). Low protein rations for the bobwhite quail. *Poultry Science* 32, 945–949. doi:10.3382/ps.0320945
- Barnes, H. J. (1987). Diseases of quail. The Veterinary Clinics of North America. Small Animal Practice 17, 1109–1144. doi:10.1016/S0195-5616(87)50107-3
- Blake, J. P., and Hess, J. B. (2013). Performance of bobwhite quail fed different levels of protein and feed additive supplementation. *Journal of Applied Poultry Research* 22, 314–318. doi:10.3382/japr.2012-00685
- Boren, J. C., Lochmiller, R. L., Leslie, D. M., Jr, and Engle, D. M. (1995).
 Amino acid concentrations in seed of preferred forages of bobwhites.
 Journal of Range Management 48, 141–144. doi:10.2307/4002801
- Brennan, L. A. (1991). How can we reverse the northern bobwhite quail decline? Wildlife Society Bulletin 19, 544–555.
- Brennan, L. A. (Ed.) (2007). 'Texas quails: ecology and management.' (Texas A&M University Press: College Station, TX, USA.)
- Brennan, L. A. (2015). Hunters are a fundamental component of northern bobwhite quail conservation. *The International Journal of Environmen*tal Studies 72, 830–838. doi:10.1080/00207233.2015.1082802
- Brennan, L. A., Hernández, F., and Bryant, F. C. (2007). Introduction. In 'Texas quails: ecology and management'. (Ed. L. A. Brennan.) pp. 2–5. (Texas A&M University Press: College Station, TX, USA.)
- Brown, S. M., and Hayslette, S. E. (2019). Effects of a Milo Diet, Mineral Supplementation, and Native Seed Use in Pen-Raised Northern Bobwhites. *Journal of the Southeastern Association of Fish and Wildlife* Agencies 6, 107–110.
- Buckley, B. R., Andes, A. K., Grisham, B. A., and Dabbert, C. B. (2015). Effects of broadcasting supplemental feed into roadside vegetation on home range and survival of female northern bobwhite. *Wildlife Society Bulletin* 39, 301–309. doi:10.1002/wsb.533
- Buckley, B. R., Andes, A. K., and Dabbert, C. B. (2018). Effects of food supplementation on the nesting dynamics of wild northern bobwhite. *Wildlife Biology* 2018, 1–8. doi:10.2981/wlb.00385
- Burger, L. W., Miller, D. A., and Southwick, R. I. (1999). Economic impact of northern bobwhite hunting in the southeastern United States. Wildlife Society Bulletin 27, 1010–1018.

- Butcher, G. (2007). Common birds in decline: a state of the birds report. Audubon Magazine. Available at https://www.audubon.org/sites/default/files/documents/sotb_cbid_magazine.pdf [verified 1 January 2020].
- Cain, J. R., Beasom, S. L., Rowland, L. O., and Rowe, L. D. (1982). The effects of varying dietary phosphorus on breeding bobwhites. *The Journal of Wildlife Management* 46, 1061–1065. doi:10.2307/3808241
- Collins, F. W. (1956). Artificial feeders: quail management techniques. Kentucky Happy Hunting Ground 12, 29.
- Cook, M. E. (1991). Nutrition and the immune response of the domestic fowl. Critical Reviews in Poultry Biology 3, 167–189.
- Dalloul, R. A., Lillehoj, H. S., Shellem, T. A., and Doerr, J. A. (2002). Effect of vitamin A deficiency on host intestinal immune response to *Eimeria acervulina* in broiler chickens. *Poultry Science* 81, 1509–1515. doi:10.1093/ps/81.10.1509
- DeMaso, S. J., Parry, E. S., Cox, S. A., and Peoples, A. D. (1998). Cause-specific mortality of northern bobwhites on an area with quail feeders in western Oklahoma. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **52**, 359–366.
- DeMaso, S. J., Townsend, I. I., Cox, S. A., Parry, E. S., and Lochmiller, R. S. (2002). The effect of quail feeders on northern bobwhite density in western Oklahoma. *National Quail Symposium Proceedings* 5, 241–244.
- DeWitt, J. B., Nestler, R. B., and Derby, J. V., Jr (1949). Calcium and phosphorus requirements of breeding bobwhite quail. *The Journal of Nutrition* 39, 567–577. doi:10.1093/jn/39.4.567
- Doerr, T. B., and Silvy, N. J. (2002). Effects of supplemental feeding on northern bobwhite populations in south Texas. *National Quail Sympo*sium Proceedings 5, 233–240.
- Doerr, T. B., and Silvy, N. J. (2006). Effects of supplemental feeding on physiological condition of northern bobwhite in south Texas. *The Journal of Wildlife Management* 70, 517–521. doi:10.2193/0022-541X(2006)70[517:EOSFOP]2.0.CO;2
- Dumke, R. T. (1982). 'Habitat development for bobwhite quail on private lands in Wisconsin.' University of Wisconsin Department of Natural Resources Technical Bulletin 128. (University of Wisconsin: Madison, WI, USA.)
- Edminster, F. C. (1954). 'American game birds of field and forest.' (Charles Scribner's Sons: New York, NY, USA.)
- Ellis, J. A., Edwards, W. R., and Thomas, K. P. (1969). Responses of bobwhites to management in Illinois. *The Journal of Wildlife Manage*ment 33, 749–762. doi:10.2307/3799303
- Frye, O. E. (1954). Studies of automatic quail feeders in Florida. *Transactions of the North American Wildlife Conference* **19**, 298–315.
- Giuliano, W. M., Lutz, R. S., and Patiño, R. (1996). Reproductive responses of adult female northern bobwhite and scaled quail to nutritional stress. *The Journal of Wildlife Management* 60, 302–309. doi:10.2307/3802228
- Godbois, I. A., Conner, L. M., and Warren, R. J. (2004). Space-use patterns of bobcats relative to supplemental feeding of northern bobwhites. *The Journal of Wildlife Management* 68, 514–518. doi:10.2193/0022-541X(2004)068[0514:SPOBRT]2.0.CO;2
- Guthery, F. S. (1997). A philosophy of habitat management for northern bobwhites. The Journal of Wildlife Management 61, 291–301. doi:10.2307/3802584
- Guthery, F. S. (2002). 'The technology of bobwhite management: the theory behind the practice.' (Iowa State Press: Ames, IA, USA.)
- Guthery, F. S., Hiller, T. L., Puckett, W. H., Jr, Baker, R. A., Smith, S. G., and Rybak, A. R. (2004). Effects of feeders on dispersion and mortality of bobwhites. *Wildlife Society Bulletin* 32, 1248–1254. doi:10.2193/0091-7648(2004)032[1248:EOFODA]2.0.CO;2
- Haines, A. M., Hernández, F., Henke, S. E., and Bingham, R. L. (2004). Effects of road baiting on home range and survival of northern bobwhites in southern Texas. *Wildlife Society Bulletin* 32, 401–411. doi:10.2193/ 0091-7648(2004)32[401:EORBOH]2.0.CO;2
- Harveson, L. A., Guthery, F. S., and Hellgren, E. C. (2004). Invertebrate consumption by breeding northern bobwhites and its relation to

- production. *The Southwestern Naturalist* **49**, 472–477. doi:10.1894/0038-4909(2004)049<0472:ICBBNB>2.0.CO;2
- Haugen, A. O. (1957). Quail and quail feeders. *Alabama Conservation* 29, 4–9.
 Henson, K. D., Rollins, D., Lyons, E. K., and Ransom, D., Jr (2012). Species visitation at free-choice quail feeders in west Texas. *Wildlife Society Bulletin* 36, 735–740. doi:10.1002/wsb.209
- Hernández, F., and Guthery, F. S. (2012). 'Beef, brush, and bobwhites: quail management in cattle country.' (Texas A&M University Press: College Station, TX, USA.)
- Hernández, F., and Peterson, M. J. (2007). Northern bobwhite ecology and life history. 'Texas quails: ecology and management'. (Ed. L. A. Brennan.) pp. 40–64. (Texas A&M University Press: College Station, TX, USA.)
- Hernández, F., Brennan, L. A., DeMaso, S. J., Sands, J. P., and Wester, D. B. (2013). On reversing the northern bobwhite population decline: 20 years later. *Wildlife Society Bulletin* 37, 177–188. doi:10.1002/wsb.223
- Hiller, T. L., and Guthery, F. S. (2004). Correlates of fall-spring mass dynamics of northern bobwhites. *The Wilson Journal of Ornithology* 116, 324–329.
- Humphrey, B. D., and Klasing, K. C. (2004). Modulation of nutrient metabolism and homeostasis by the immune system. World's Poultry Science Journal 60, 90–100. doi:10.1079/WPS20037
- Johnson, J. L., Rollins, D., and Reyna, K. S. (2012). What's a quail worth? A longitudinal assessment of quail hunter demographics, attitudes, and spending habits in Texas. *National Quail Symposium Proceedings* 7, 294–299.
- Klasing, K. C. (2007). Nutrition and the immune system. British Poultry Science 48, 525–537. doi:10.1080/00071660701671336
- Klasing, K. C., and Korver, D. R. (2019). Nutritional diseases. In 'Diseases of poultry'. (Ed. D. E. Swayne.) pp. 1255–1285. (Wiley Blackwell: Hoboken, NJ, USA.)
- Kogut, M. H., and Klasing, K. C. (2009). An immunologist's perspective on nutrition, immunity, and infectious diseases: introduction and overview. *Journal of Applied Poultry Research* 18, 103–110. doi:10.3382/japr. 2008-00080
- Koutsos, E. A., and Klasing, K. C. (2001). Interactions between the immune system, nutrition and productivity of animals. In 'Recent advances in animal nutrition'. (Ed. P. C. Garnsworthy and J. Wiseman.) pp. 173–190. (Nottingham University Press: UK.)
- Lehmann, V. W. (1953). Bobwhite population fluctuations and vitamin A. Transactions of the North American Wildlife Conference 18, 199–246.
- Leopold, A. (1933). 'Game Management.' 1946, reprint. (Charles Scribner's Sons: New York, NY, USA.)
- Madison, L. A., Robel, R. J., and Jones, D. P. (2000). Influence of food plots on northern bobwhite movements, habitat use, and home range. *National Quail Symposium Proceedings* 4, 36–41.
- Madison, L. A., Robel, R. J., and Jones, D. P. (2002). Hunting mortality and overwinter survival of northern bobwhites relative to food plots in Kansas. Wildlife Society Bulletin 30, 1120–1127.
- McGrath, D. J., Terhune, T. M., and Martin, J. A. (2017). Northern bobwhite habitat use in a food subsidized pyric landscape. *The Journal of Wildlife Management* 81, 919–927. doi:10.1002/jwmg.21254
- McLaughlin, J. W., Wiley, D. S., Dabbert, C. B., and Terhune, T. M. (2019). Broadcast supplemental feeding and northern bobwhite demographics in Texas. *The Journal of Wildlife Management* 83, 52–63. doi:10.1002/jwmg.21557
- Miller, R. S. (2011). Foraging behavior of northern bobwhite in relation to resource availability. Thesis, Mississippi State University, Starkville, MS, USA.
- Morris, G. A. I. L., Conner, L. M., and Oli, M. K. (2010). Use of supplemental northern bobwhite (*Colinus virginianus*) food by nontarget species. *Florida Field Naturalist* 38, 99–105.
- National Research Council (1994). 'Nutrient requirements of poultry: 1994.' 9th edn. (National Academy of Science: Washington, DC, USA.)

- Nestler, R. B. (1946). Vitamin A, vital factor in the survival of bobwhites. Transactions of the North American Wildlife Conference 11, 176–192.
- Nestler, R. B. (1949). Nutrition of bobwhite quail. *The Journal of Wildlife Management* 13, 342–358. doi:10.2307/3795628
- Nestler, R. B., and Bailey, W. W. (1943). Vitamin A deficiency in bobwhite quail. *The Journal of Wildlife Management* 7, 170–173. doi:10.2307/ 3795721
- Nestler, R. B., Bailey, W. W., and McClure, H. E. (1942). Protein requirements of bobwhite quail chicks for survival, growth, and efficiency of feed utilization. *The Journal of Wildlife Management* 6, 185–193. doi:10.2307/3795900
- Nestler, R. B., Bailey, W. W., Llewellyn, L. M., and Rensberger, M. J. (1944a). Winter protein requirements of bobwhite quail. *The Journal of Wildlife Management* 8, 218–222. doi:10.2307/3795701
- Nestler, R. B., Bailey, W. W., Rensberger, M. J., and Benner, M. Y. (1944b).
 Protein requirements of breeding bobwhite quail. *The Journal of Wildlife Management* 8, 284–289. doi:10.2307/3796021
- Nestler, R. B., DeWitt, J. B., Derby, J. V., and Moschler, M. (1948). Calcium and phosphorus requirements of bobwhite quail chicks. *The Journal of Wildlife Management* 12, 32–36. doi:10.2307/3795743
- Nice, M. M. (1910). Food of the bobwhite. *Journal of Economic Entomology* 3, 295–313. doi:10.1093/jee/3.3.295
- Norris, L. C. (1935). Nutrition of game birds. New York State Conservation Department Annual Report 331–338.
- North American Bird Conservation Initiative (NABCI) (2019). 2019 state of the birds: America's birds are in crisis. Available at https://www.stateofthebirds.org/2019/wp-content/uploads/2019/09/2019-State-of-the-Birds.pdf [verified 1 January 2020].
- Parsons, D. S., Whiting, R. M., Jr, Liu, X., and Dietz, D. R. (2000). Food plot use by juvenile northern bobwhites in east Texas. *National Quail Symposium Proceedings* 4, 71–74.
- Peoples, A. D., Lochmiller, R. L., Boren, J. C., Leslie, D. M., Jr, and Engle, D. M. (1994a). Limitations of amino acids in diets of northern bobwhites (*Colinus virginianus*). *American Midland Naturalist* 132, 104–116. doi:10.2307/2426205
- Peoples, A. D., Lochmiller, R. L., Leslie, D. M., Jr, Boren, J. C., and Engle, D. M. (1994b). Essential amino acids in northern bobwhite foods. *The Journal of Wildlife Management* 58, 167–175. doi:10.2307/3809564
- Purvis, J. (2011). 'Small game harvest surveys, 1981–2010.' (Texas Parks and Wildlife Department: Austin, TX, USA.)
- Robel, R. J. (1969). Food habits, weight dynamics, and fat content of bobwhites in relation to food plantings in Kansas. *The Journal of Wildlife Management* 33, 237–249. doi:10.2307/3799823
- Robel, R. J. (1972). Body fat content of bobwhites in relation to food plantings in Kansas. National Quail Symposium Proceedings 1, 139–149.
- Robel, R. J., and Kemp, K. E. (1997). Winter mortality of northern bobwhites: effects of food plots and weather. *The Southwestern Natural*ist 42, 59–67.
- Robel, R. J., Case, R. M., Bisset, A. R., and Clement, T. M., Jr (1974). Energetics of food plots in bobwhite management. *The Journal of Wildlife Management* 38, 653–664. doi:10.2307/3800032
- Rolland, V., Hostetlesouthr, J. A., Hines, T. C., Percival, H. F., and Oli, M. K. (2011). Factors influencing reproductive performance of northern bobwhite in South Florida. *European Journal of Wildlife Research* 57, 717– 727. doi:10.1007/s10344-010-0479-5
- Rollins, D. (2002). Sustaining the 'quail wave' in the southern Great Plains. *National Quail Symposium Proceedings* **5**, 48–56.
- Rollins, D. (2007). Quails on the Rolling Plains. In 'Texas quails: ecology and management'. (Ed. L. A. Brennan.) pp. 117–141. (Texas A&M University Press: College Station, TX, USA.)
- Rosene, W. (1969). 'The Bobwhite Quail.' (Rutgers University Press: New Brunswick, NJ, USA.)
- Sauer, J. R., Pardieck, K. L., Ziolkowski, D. J., Jr, Smith, A. C., Hudson, M. A. R., Rodriguez, V., Berlanga, H., Niven, D. K., and Link, W. A.

- (2017). The first 50 years of the North American breeding bird survey. *The Condor: Ornithological Applications* **119**, 576–593. doi:10.1650/CONDOR-17-83.1
- Sauvant, D., Perez, J. M., and Tran, G. (Eds) (2004). 'Tables of composition and nutritional value of feed materials: pigs, poultry, cattle, sheep, goats, rabbits, horses and fish.' (Wageningen Academic Publishers: Paris, France)
- Schultz, V. (1948). Vitamin A as a survival factor of the bob-white quail (Colinus v. virginianus) in Ohio during the winter of 1946–47. The Journal of Wildlife Management 12, 251–263.
- Scott, M. L., Holm, E. R., and Reynolds, R. E. (1958). A study of the phosphorus requirements of young bobwhite quail. *Poultry Science* 37, 1425–1428. doi:10.3382/ps.0371425
- Scott, M. L., Holm, E. R., and Reynolds, R. E. (1963). Studies on the protein and methionine requirements of young Bobwhite quail and young ringnecked pheasants. *Poultry Science* 42, 676–680. doi:10.3382/ps. 0420676
- Scott, M. L., Holm, E. R., and Reynolds, R. E. (1964). Studies on the pantothenic acid and unidentified factor requirements of young ringnecked pheasants and bobwhite quail. *Poultry Science* 43, 1534–1539. doi:10.3382/ps.0431534
- Serafin, J. A. (1974). Studies on the riboflavin, niacin, pantothenic acid and choline requirements of young Bobwhite quail. *Poultry Science* 53, 1522–1532. doi:10.3382/ps.0531522
- Serafin, J. A. (1977). Studies on the protein and sulfur amino acid requirements of young bobwhite quail. *Poultry Science* 56, 577–585. doi:10.3382/ps.0560577
- Serafin, J. A. (1982). Influence of protein level and supplemental methionine in practical rations for young endangered masked bobwhite quail. *Poultry Science* 61, 988–990. doi:10.3382/ps.0610988
- Singh, A., Hines, T. C., Hostetler, J. A., Percival, H. F., and Oli, M. K. (2011). Patterns of space and habitat use by northern bobwhites in South Florida, USA. *European Journal of Wildlife Research* 57, 15–26. doi:10.1007/s10344-010-0393-x
- Sisson, D. C., Stribling, H. L., and Speake, D. W. (2000). Effects of supplemental feeding on home range size and survival of northern bobwhites in South Georgia. *National Quail Symposium Proceedings* 4, 128–131.
- Stoddard, H. L. (1931). 'The bobwhite quail: its habits, preservation and increase.' (Charles Scribner's Sons: New York, NY, USA.)
- Stribling, H. L., and Sisson, D. C. (2009). Hunting success on Albany, Georgia plantations: the Albany Quail Project's modern quail management strategy. *National Quail Symposium Proceedings* 6, 338–347.
- Swayne, D. E. (2019). 'Diseases of poultry.' 14th edn. (Wiley Blackwell: Hoboken, NJ, USA.)

- Townsend, D. E., Lochmiller, R. L., DeMaso, S. J., Leslie, D. M., Jr, Peoples, A. D., Cox, S. A., and Parry, E. S. (1999). Using supplemental food and its influence on survival of northern bobwhite (*Colinus virginianus*). *Wildlife Society Bulletin* 27, 1074–1081.
- Tri, A. N., Hernandez, F., Hewitt, D. G., Kuvlesky, W. P., Jr, and Brennan, L. A. (2012). Effects of Carbohydrate-Based and Protein–Carbohydrate Rations on Wild Bobwhite Nesting and Harvest Demographics. *National Quail Symposium Proceedings* 7, 101–106.
- Tri, A. N., Brennan, L. A., Hernández, F., Kuvlesky, W. P., Jr, and Hewitt, D. G. (2014). Home ranges of breeding northern bobwhite hens in south Texas with access to supplemental feed. *Bulletin of the Texas Ornithological Society* 47, 11–16.
- Turner, A. S., Conner, L. M., and Cooper, R. J. (2008). Supplemental feeding of northern bobwhite affects red-tailed hawk spatial distribution. *The Journal of Wildlife Management* 72, 428–432. doi:10.2193/2006-303
- U.S. Geological Survey (USGS) (2020). State Wildlife Action Plans. Available at https://www1.usgs.gov/csas/swap/index.html [verified 1 January 2020].
- Wellendorf, S. D., Palmer, W. E., and Bostick, A. M., III (2017). Effects of Supplemental Feeding on Breeding Season Home Ranges and Resource Selection of Northern Bobwhites. *National Quail Symposium Proceedings* 8, 187–195.
- Whitelaw, R. E., Palmer, W. E., Wellendorf, S. D., and Carroll, J. P. (2009). Effect of supplemental feeding on winter diet and body mass of northern bobwhites. *National Quail Symposium Proceedings* 6, 282–289.
- Wiley, D. S. S. (2017). Northern bobwhite reproduction in the Rolling Plains of Texas. M.Sc. Thesis, Texas Tech University, Lubbock, TX, USA.
- Williams, C. K., Guthery, F. S., Applegate, R. D., and Peterson, M. J. (2004). The northern bobwhite decline: scaling our management for the twenty-first century. *Wildlife Society Bulletin* **32**, 861–869. doi:10.2193/0091-7648(2004)032<0861:TNBDSO>2.0.CO;2
- Wilson, H. R., Douglas, C. R., and Nesbeth, W. G. (1977). Feed consumption and protein efficiency by bobwhite quail in response to dietary energy levels. *Poultry Science* **56**, 1127–1129. doi:10.3382/ps.0561127
- Wilson, H. R., Holland, M. W., Jr, and Harms, R. H. (1972). Dietary calcium and phosphorus requirements for bobwhite chicks. *The Journal of Wildlife Management* 36, 965–968. doi:10.2307/3799459
- Wood, K. N., Guthery, F. S., and Koerth, N. E. (1986). Spring-summer nutrition and condition of northern bobwhites in south Texas. *The Journal of Wildlife Management* 50, 84–88. doi:10.2307/3801492

Handling Editor: Weihong Ji