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Dear Mr. Pinder-Moss

Please find enclosed a copy of my M.Sc. thesis entitled "Flight Speeds and Energetics of Seven Bird Species". At present, I do not know of any other research that has been done on this reserve or on any others, but I will let you know if I discover any. Thank you for your interest.

Sincerely,

Rebecca Kolotylo

Rebecca Kolotylo

enclosure

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JPM

FLIGHT SPEEDS AND ENERGETICS OF SEVEN BIRD SPECIES

By

REBECCA ANN KOLOTYLO

B.Sc., The University of British Columbia, 1987

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

in

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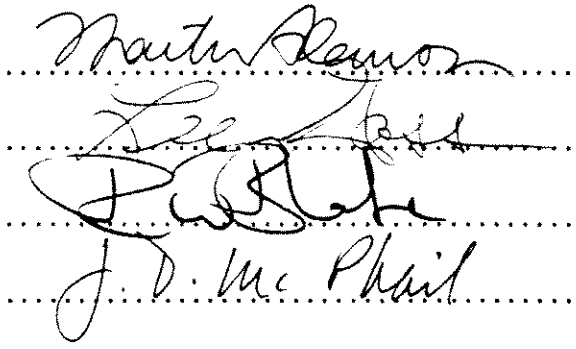
(Department of Zoology)

We accept this thesis as conforming

to the required standard



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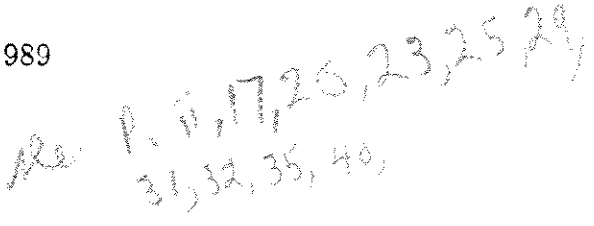

ABSTRACT

Flight speeds of seven bird species, the Tree Swallow (*Tachycineta bicolor*), Mountain Bluebird (*Sialia currucoides*), White-throated Swift (*Aeronautes saxatalis*), European Starling (*Sturnus vulgaris*), Black Tern (*Chlidonias nigra*), Pigeon Guillemot (*Cepphus columba*), and Red-necked Grebe (*Podiceps grisegna*), were recorded using a Doppler radar handgun. Velocities were measured of adult birds flying to and from foraging areas while rearing young, and totalled 1178 records. Morphological measurements were also made on some of the species and were used, along with literature values, to construct curves of estimated total power required for flight versus flight velocity for each species. The mean observed flight speed, V_{obs}, for each species was then compared to the minimum power speed, V_{mp}, and the maximum range speed, V_{mr}, on the power curve. For five of the seven study species, the V_{obs} was significantly greater than V_{mr}, and thus appeared to be independent of morphology, foraging methods and habitats. The V_{obs} of the other two species was found to be between V_{mp} and V_{mr} for the Pigeon Guillemot and less than V_{mp} for the Red-necked Grebe.

In a more detailed study of the Tree Swallow and the Mountain Bluebird, V_{obs} was determined to be fairly constant over the recording period. Individual power curves were constructed for five female Mountain Bluebirds and three female Tree Swallows, since both morphological measurements and flight speeds were recorded for these individuals. In each case, V_{obs} was significantly greater than V_{mr}. For the bluebird, it was also found that the number of visits to the nest per hour per nestling did not appear to increase with the age of the nestling. The rate of feedings, however, was quite variable for both the Tree Swallow and Mountain Bluebird. By setting the observed flight speed, V_{obs}, equal to a predicted optimal speed, V_{opt}, the net rate of energy gain during foraging by the parents could be determined. Comparing this energy gain with estimates of nestling energy requirements for both species resulted in the conclusion that the observed speed could not be the same as the optimal speed, and that in order to meet nestling requirements, the parents may increase their feeding rate during other parts of the day not under observation.

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CHAPTER ONE

GENERAL INTRODUCTION

Bird flight can be studied using many different approaches, including investigations of anatomy, morphology, and physiology. General principles of avian morphology (including the evolution of flight, the central nervous system, the cardiovascular system, the respiratory system, and structural adaptations for flight) are discussed by King and King (1979) and a general discussion on energy expenditures and intakes can be found in Wolf and Hainsworth (1978). Detailed analysis of the anatomy involved in locomotion can be found in Raikow (1985). The metabolic costs of flight have been studied extensively by Tucker (1968, 1972, 1973) and others (*e.g.* Bernstein *et al.*, 1973; Torre-Bueno and Larochelle, 1978; Hails, 1979; Hails and Bryant, 1979; Bryant and Westerterp, 1980; Flint and Nagy, 1984; Westerterp and Bryant, 1984; Rothe and Nachtigall, 1985; Rothe *et al.*, 1987). Respiratory mechanics, gas exchange, circulation, temperature regulation, water loss and energy turnover in migratory flights are discussed by Berger and Hart (1974). Specific classification of avian muscles and muscle fibre types can be found in George and Berger (1966) and Rosser and George (1986).

The aerodynamic approach concentrates mainly on how physical design influences the cost of flight. Early work on flight mechanics was mainly descriptive (*e.g.* Brown, 1948, 1953). Estimations of the varing aerodynamic costs of flight with changing flight speeds come from the momentum jet theory (Pennycuick, 1968a,*b*, 1969, 1975, 1989) as well as from the vortex theory (Rayner, 1979a,*b*,*c*). Records of flight speeds range from early estimates using speedometers in automobiles and airplanes (Cooke, 1933; Meinertzhagen, 1955) to more accurate measurements using ornithodolites (Pennycuick, 1987) and radar (Schnell 1965, 1974; Schnell and Hellack 1978, 1979; Blake *et al.*, 1989).

The speed at which a bird flies depends upon the reason for the flight as well as environmental conditions such as food supply, time, and predation risk. Curves of the aerodynamic power required for flight versus flight velocity indicate optimal speeds in

particular circumstances, but collections of flight speed data (Gill, 1985; McLaughlin and Montgomerie, 1985; Rayner, 1985*b*; Pennycuick, 1987; Blake *et al.*, 1989, and others) indicate a pattern of flight speeds that is, as yet, unclear. The objective of this study is to compare a large sample of flight speed data from a range of bird species under similar conditions to predicted speeds. Chapter Two will compare observed flight speeds of seven species to optimal speeds derived from power curves, while Chapter Three will concentrate on two of the species.

A. PRINCIPLES OF POWERED FLIGHT

Flight can be categorized into several modes - passive flight, powered forward flight, and hovering. Passive flight, which includes gliding and soaring, involves minimal wing movement and is thus a low cost form of locomotion (Pennycuick 1971, 1972, 1982). This type of flight is common in larger birds such as albatrosses, eagles, vultures and gulls as well as others with opportunities to exploit updrafts, thermals, or winds (Pennycuick, 1971, 1972, 1982). Intermittent flight involves both flapping and non-flapping flight (Rayner, 1977, 1985a). Bounding intermittent flight is found mainly in small birds while undulating intermittent flight is employed by larger birds such as woodpeckers, gulls, and crows (Ward-Smith, 1984a,*b*). Other patterns of flight include formation flight (Hummel, 1983) and flying in ground effect (Withers and Timko, 1977; Blake, 1983, 1985).

Steady flapping flight requires more energy input than passive flight in terms of aerodynamic power. There have been many attempts to describe the aerodynamic power required for flight (Pennycuick 1968a,*b*, 1969, 1975, 1989; Tucker, 1973; Greenewalt, 1975; Rayner, 1979a,*b*,*c*). Pennycuick (1968a,*b*, 1969) developed the momentum jet theory, which has been modified several times (Tucker, 1973; Pennycuick, 1975, 1989). Greenewalt (1962, 1975) based his approach to flight on scaling techniques and comparisons between groups of fliers (passerines, non-passerines, hummingbirds, shorebirds, waterfowl, bats and insects).

In this study, aerodynamic power required for flight has been determined based mainly on the model developed by Pennycuick (1968a,*b*, 1969, 1975, 1989). Aerodynamic power can be divided into four components; parasite power P_{para}, profile power P_{pro}, induced power P_{ind} and basal metabolic power, P_{met}. Parasite power overcomes the pressure drag and skin friction of the bird's body, which increases with increasing flight velocity. It can be written as:

$$P_{para} = \frac{1}{2}\rho V^3 A_p C_{D(para)} \tag{1}$$

where ρ, V, A_p, and $C_{D(para)}$ are air density (kgm^{-3}), forward flight velocity of the bird (ms^{-1}), frontally projected area of body (m^2), and the parasite drag coefficient, respectively. P_{para} is measured in Watts (W).

The frontally projected area of the body can be determined if the diameter of the body at its widest point is known, using

$$A_p = \pi(\frac{d}{2})^2 \tag{2}$$

where d is the body diameter at widest point (m).

Alternatively, A_p can be determined by

$$A_p = 0.00813M^{2/3} \tag{3}$$

Pennycuick (1989, program 1), where M is the body mass (kg).

The parasite drag coefficient, $C_{D(para)}$, can be estimated based on the Reynold's number, R_e, of the body;

$$R_e = \frac{V\ell\rho}{\mu} \tag{4}$$

where ℓ is a characteristic length, V is the free stream velocity, and μ is the viscosity of the fluid. R_e can be estimated as

$$R_e = 125000M^{1/2} \tag{5}$$

(Pennycuick, 1989). If the body Reynold's number is less than $50,000$, $C_{D(para)}$ is estimated as 0.4. If $R_e > 200,000$, $C_{D(para)}$ is taken to be 0.25 (Pennycuick *et al.*, 1988, Pennycuick, 1989). Values of R_e between $50,000$ and $200,000$ result in a $C_{D(para)}$ according to

$$C_{D(para)} = 1.57 - (0.108 ln R_e) \tag{6}$$

Profile power, P_{pro}, is the power required to overcome the profile drag of the wings and is proposed to be constant by Pennycuick, (1969, 1975, 1989). Other approximations (Ward-Smith, 1984a,*b* Rayner, 1979a,*b*,*c*, Tucker, 1987) indicate that profile power increases with velocity, resulting in

$$P_{pro} = \frac{1}{2}\rho V^3 S_w C_{D(pro)} \tag{7}$$

where S_w and $C_{D(pro)}$ are the wetted surface area of the wings (m^2) and the profile drag coefficient respectively. The profile drag coefficient is generally estimated to be about 0.02 (Rayner, 1979*c*).

Induced power is the power required to overcome the weight of the bird (drag due to lift). This power requirement decreases with increasing flight velocity, as less energy is required to stay airborne at higher speeds. Induced power can be expressed as

$$P_{ind} = \frac{1.2L^2}{\frac{1}{2}\rho\pi b^2 V} \tag{8}$$

where b is the wingspan (m), 1.2 the aerofoil efficiency factor, and L, the lift, can be determined by

$$L = [(Mg)^2 + (\frac{1}{2} A_p C_{D(para)} V^2)^2]^{\frac{1}{2}} \tag{9}$$

(Pennycuick, 1989), where g is the gravitational constant of $9.81 ms^{-2}$.

The basal metabolic power, P_{met}, is given by

$$P_{met} = 0.23(6.25M^{0.724}) \tag{10}$$

for passerines and

$$P_{met} = 0.23(3.79M^{0.723}) \tag{11}$$

for non-passerines (Lasiewski and Dawson, 1967). The term of 0.23 is a conversion efficiency to convert chemical energy to mechanical work (Pennycuick, 1975).

The total aerodynamic power requirement, P_{tot}, can be written as

$$P_{tot} = 1.1(P_{para} + P_{pro} + P_{ind} + P_{met}) \tag{12}$$

The factor of 1.1 accounts for the costs of respiration and circulation (Tucker, 1973; Pennycuick, 1975, 1989).

The total power, P_{tot}, is a characteristically U-shaped curve. The minimum point on this curve is termed the minimum power speed, V_{mp}. A bird should fly at V_{mp} if its objective is to stay airborne for as long as possible (least cost per unit time). The maximum range speed, V_{mr}, is given by a tangent to the curve passing through the origin. The maximum range speed is optimal for travelling long distances (least cost per unit distance).

Noting that coefficients of drag and lift are a source of uncertainty in the momentum jet theory, Rayner (1979a,*b*,*c*) proposed a quasi-steady vortex ring theory as an alternative in describing hovering and forward flight. This method involves the distribution and kinetic energy of vortices left in the wake of the body and wings. Induced power is defined as the mean rate of increase of kinetic energy in the wake, and does not involve lift or induced drag coefficients. Profile power is based on parameters of the downstroke (stroke period, downstroke ratio, stroke amplitude, angular position of the wing). Parasite power is estimated using an indicator of size as well as drag coefficients, based on the body angle. Again, the summation of these three aerodynamic power equations gives a U-shaped curve. More recent work on wake vortices includes studies by Spedding *et al.* (1984), and Spedding (1987a,*b*).

A theoretical maximum amount of energy can be supplied to the flight muscles (Weis-Fogh and Alexander, 1977) for sustained flight, and can be expressed as

$$P_{max} = 250(0.17M^{0.97}) \tag{13}$$

The corresponding V_{max} can be determined from the power curve, and is thus the maximum flight speed available to the bird.

The stalling speed of a bird, V_{stall}, can also be determined. The stalling speed is the velocity at which flow separation occurs on the top surface of the wing, causing a sudden decrease in lift and increase in drag. V_{stall} can be defined as

$$V_{stall} = (\frac{2Mg}{C_{L(max)}\rho S_w})^{\frac{1}{2}} \tag{14}$$

where $C_{L(max)}$ is the maximum lift coefficient.

Plots of power required for flight versus flight velocity based on metabolic studies have tended to be rather flat (Tucker, 1972; Bernstein *et al.*, 1973; Torre-Bueno and Larochelle, 1978; Berger, 1985), although some recent work (Rothe *et al.*, 1987) has resulted

in U-shaped power curves. Independent approaches to estimating the mechanical power requirements for flight (momentum jet, vortex theories) have resulted in U-shaped curves, and are based on sound aerodynamic principles. The relationship between muscle efficiency and flight velocity has not been studied. This is unfortunate because it may provide insights on the difference between mechanical and metabolic power necessary for flight.

B. HISTORY OF FLIGHT SPEED RECORDS

Bird flight velocities have been measured for many years and the speeds at which birds fly has interested many biologists. Speeds have been recorded using various methods, many of which are inaccurate and unreliable. Early attempts at estimating flight speeds produced some results that are difficult to believe, such as a $200mph$ ($90ms^{-1}$) record for a swift (*Chaetura*) by Stuart-Baker (in Meinertzhagen, 1955).

Early collections of flight records (*e.g.* Cooke, 1933; Cottam *et al.*, 1942; and Meinertzhagen, 1955) include observations made by automobile speedometers, theodolites, airspeed indicators of airplanes, homing experiments, trains, kites, stopwatches, rangefinders, and estimations from ships and mailboats. Most measurements were made without reference to wind speed and direction or to environmental conditions, although in some cases (Broun and Goodwin, 1943), wind speeds and directions were measured with flight speeds, but the records remained merely as published lists. As well, many records were obtained by "chasing"a bird with a vehicle, which resulted in an estimation of a maximum flight speed, not of normal routine flight activity. Flight speed records obtained using such methods are generally unreliable estimates and the sample number is usually low, because of the time required to measure the speeds. The use of stopwatches over a known distance, however, is still a common method (e.g. Bryant and Turner, 1982; Gill, 1985; McLaughlin and Montgomerie, 1985; Tatner and Bryant, 1986).

Many studies have been conducted using wind tunnels to evaluate bird flight and its costs (Pennycuick, 1968a,*b*; Tucker, 1968, 1972; Bernstein *et al.*, 1973; Torre-Bueno and Larochelle, 1978). Flight in wind tunnels may involve air turbulences and distortions due

to interference with tunnel walls, redistribution of a bird's shape and weight while wearing a respiratory mask, and also lacks natural wind currents and any environmental cues a bird would normally experience. The flight pattern of a pigeon in a wind tunnel, for example, varies from that of a free flying bird (Butler *et al.*, 1977). The duration of wing flapping periods in free-ranging pigeon flights was found to be longer than in wind tunnel flights. As well, take-off and landing kinematics differed between wind tunnel and free-ranging flights. Although wind tunnel studies may establish a range of velocities at which a particular bird will fly (for example, Torre-Bueno and Larochelle, 1978), they do not necessarily reflect natural flight velocities.

Lanyon (1962) introduced the Doppler radar unit into the field, which has been used extensively (Schnell, 1965, 1974; Schnell and Hellack, 1978, 1979). Schnell's equipment consisted of a five-part system, including a transmitter, transmitting antenna, a mixer to compare reflected and transmitted waves, and a receiver. This radar unit was calibrated to 2 miles per hour intervals. Recording flight velocities via Doppler radar is a rapid way to collect a large sample size (Blake *et al.*, 1989). Schnell (1965) notes that he recorded more flight speeds in two summers than the total number that had previously been recorded in the literature. Rayner (1985*b*) also suggests that Doppler radar is probably the best method to obtain flight speed records.

As well as recording accurate speeds of birds flying parallel to the unit, doppler radar records speeds at angles $\pm 20°$ to the gun that are not significantly different from the true speeds found when the angle is corrected for (Schnell, 1965; Blake *et al.*, 1989). A more portable doppler radar unit, such as the modified radar handgun used by Blake *et al.* (1989) is easier and more convenient to use than Schnell's unit, because it can be easily aimed at a particular bird rather than waiting for one to fly in parallel to it. As well, at angles greater than or equal to $30°$, objects of the size of birds are not detected by the radar handgun, and thus almost all speeds recorded can be assumed to be not significantly different from the bird's true speed.

C. FLIGHT STRATEGIES

The characteristic predicted "optimal" speeds from the power curve, V_{mp} and V_{mr} should be considered optimal only under certain conditions. V_{mp} is optimal when a bird wants to travel for the longest amount of time on a given amount of fuel. Flight at this speed would be expected when time is not a constraint or, for example, while searching for food when the food supply is low or uncertain (Rayner, 1985*b*; Pennycuick, 1975). Swifts in their roosting flights at night are thought to fly at V_{mp} (Pennycuick, 1987). V_{mr} should be chosen when there is an advantage to travelling the greatest distance with a set amount of fuel. For example, birds flying back and forth to a foraging area should fly at V_{mr}, as should birds on migration (Pennycuick, 1975; Rayner, 1985*b*). Under other circumstances, different speeds may be considered more favourable.

Norberg (1981) proposed that flight speeds of parents feeding young should be greater than V_{mr} in order to bring the most food to the young. Female Lapland longspurs (*Calcarius lapponicus*) feeding young, however, did not fly faster than V_{mr} (McLaughlin and Montgomerie, 1985). McLaughlin and Mongomerie suggest that brood size may be a factor in determining air speed. For instance, when brood size is less than a maximum number, there may not be any advantage to flying above V_{mr}.

Another reason for flying at velocities other than the characteristic speeds was proposed by Gill (1985). Gill found that Long-tailed Hermit hummingbirds (*Phaethornis superciliosus*) fly at an average speed of $11.6ms^{-1}$ between foraging sites, a value significantly greater than the V_{mr} value of $7.5ms^{-1}$. He attributes this higher than expected flight velocity to a gain in time savings, thereby allowing more visits to flowers (a greater energy gain) or more time for lekking activities (a reproductive gain). As well, Gill (1985) notes that there is competition for flowers so there is an advantage to arriving first.

The optimum speed for travel may be that velocity which a bird can maintain the longest, and which was found to be the minimum power speed for the bat *Pteropus poliocephalus* flying in a wind tunnel (Carpenter, 1985). Carpenter stated that it should

not be assumed that an animal's flight speed is limited only by available fuel or that a bird will fly at its least costly velocity. He proposed that if birds did fly at V_{mp} it may be because that is simply the least strenuous speed.

The flight of most Procellariiformes consists of both flapping and gliding phases, and is termed flap-gliding. Pennycuick (1987), in recent comparisons of flight between northern and southern seabirds, suggested that the flapping speed of flap-gliding birds should be reasonably efficient and close to the best gliding speed. Pennycuick determined that the average flapping or flap-gliding velocity of the birds recorded lay between V_{mp} and V_{mr}, and did not significantly optimize either speed.

Kestrels (*Falco tinnunculus*) trained to fly in a corridor were found to fly near maximum range speed when the birds were not loaded, while when loaded with an extra $0.6N$ of body weight, their flight speeds decreased to nearly the predicted minimum power speed (Videler *et al.*, 1988a,*b*). The approximately 10% decrease of flight speed with an increase in load is contrary to predictions of greater V_{mp} and V_{mr} with increasing mass. Videler *et al.* (1988a,*b*) suggest that the birds appear to change their flight strategy from flying at V_{mr} to V_{mp}, as well as altering their wingbeat kinematics, when their load is increased.

Other flight studies in wind tunnels (*e.g.* Torre-Bueno and Larochelle, 1978; Rothe and Nachtigall, 1985) result in birds flying at speeds that may not necessarily be equivalent to ones chosen in the field under natural conditions.

White ibises (*Eudocimus albus*) were found to fly at speeds above the V_{mp} values but far below V_{mr} on their way to and from foraging sites. These observations were made with an ornithodolite system during the early breeding season, before the eggs were hatched (Pennycuick and de Santo, 1989).

Blake *et al.* (1989) found that barn swallows (*Hirundo rustica*) flew at speeds greater than V_{mr}. Recorded flight speeds were divided into two groups based on flight behaviour. The first group flew close to the ground ($< 0.5m$ above ground level) and in a straight line, and had a mean velocity of $8.6ms^{-1}$. The flight of the second group was $\geq 0.5m$ above ground level and not as straight as the first group, and had a mean flight velocity

of $6.8ms^{-1}$. The means of both groups were significantly higher than the predicted $V_{mp}(4.2ms^{-1})$ and $V_{mr}(5.6ms^{-1})$.

The development of a biomechanical model such as the one described for flight is useful in that its predictions can be tested ecologically and may provide helpful insights into the considerations and constraints of specific ecological situations. In particular, the consequences of flying at velocities other than V_{mr}, for example, will have certain implications for adult birds depending on their circumstances and reason for the flight. In view of the variety of results from the above mentioned studies, it appears that bird flight velocities vary in their relation to predicted velocities. The circumstances of each study, however, also vary, and most describe separate situations.

THIS STUDY

Most studies of bird flight speeds have been performed using only a single species with small samples, and each study carried out under different conditions. As well, theories leading to calculations of the minimum power and maximum range speeds may vary between studies, as will the technique of measuring the flight speed. Therefore, in terms of determining flight speeds, it would be useful if a large sample size of flight speed recordings could be collected for a range of species using only one reliable and accurate recording technique, and these speeds compared with predicted optimal speeds that were all similarily calculated. As well, the flight speeds should be collected under similar circumstances, in order to test for a particular result and compare between species and possibly within species. The above proposals are the objective of this thesis.

The following two chapters describe studies of Doppler radar flight speed recordings of seven species of birds ranging in size from $20g$ to $1.0kg$. The flight velocities were measured during the breeding season for all birds, and under similar conditions - little or no wind, a clear flight path, and a knowledge of the purpose of the flight. All measurements were taken using the same equipment. Chapter Two includes flight speeds recorded for all of the study species. Wing and body dimensions were either determined in the field or

taken from museum specimens or literature sources. These were used to calculate power curves for each species in order to compare observed and predicted speeds. Chapter Three concentrates on two of the species, for which a more detailed analysis was done. Feeding rates and adult flight speeds in relation to the age and number of nestling were recorded. Power curves were constructed for some individual birds to compare observed and predicted speeds. Nestling energy requirements were estimated and the resulting energy delivery rate compared to actual velocities.

CHAPTER TWO

OBSERVED VERSUS PREDICTED FLIGHT SPEEDS

2.1 INTRODUCTION

In order to make comparisons between observed flight speeds and predicted speeds for a number of species, a specific condition was chosen to be constant for each study site, that the flight speeds recorded would be obtained from birds flying to or from a foraging site while raising nestlings. Velocities were recorded with a hand held Doppler radar gun (Blake *et al.*, 1989). In five of the seven species, large sample sizes (ranging from 100 to over 300 speeds per species) were obtained, while the other two samples were of 41 and 64 records respectively.

The birds studied represent seven different Families from four Orders: Passeriformes, Apodiformes, Charadriiformes, and Podicipediformes. Particular species were chosen based mainly on their morphology, to ensure that a range of wing and body dimensions were included. Choice was limited, however, by the availability, accessibility and suitability of the species for radar recordings. The study species included: Tree Swallow (*Tachycineta bicolor*), Mountain Bluebird (*Sialia currucoides*), European Starling (*Sturnus vulgaris*), White-throated Swift (*Aeronautes saxatalis*), Black Tern (*Chlidonias nigra*), Pigeon Guillemot (*Cepphus columba*), and Red-necked Grebe (*Podiceps grisegena*).

The Tree Swallow and the White-throated Swift are both aerial insectivores. The swallow forages preferably over water and nests in holes in trees, while the swift forages over varied types of mountainous terrain and builds nests in cliff and canyon crevices. The Mountain Bluebird is also an insectivore but catches prey found on the ground. It often hovers above the ground, presumably looking for prey items, before dropping to the ground or continuing its flight. It can be found mainly in open rangelands and meadows, where it nests in tree cavities or nestboxes. The Black Tern, which is found nesting in marshes and lakes, feeds on insects that it catches while flying, but it also preys on small fish. The Pigeon Guillemot and Red-necked Grebe also eat fish, which they catch by diving under

the water. Their habitats, however, are quite different. The guillemot is found nesting in rock cliffs of coastal islands and is thus a marine bird. The grebe breeds mainly on shallow lakes and inland marshes. The European Starling is a widespread species common in many habitats. It is chiefly a ground forager on insects but also eats some small fruits, and nests in tree cavities, cliffs, or buildings.

It was possible to obtain morphological measurements for some of the species in the field, while other measurements were taken from museum specimens or literature sources. Using these dimensions, aerodynamic power required for flight versus flight velocity could be plotted for each species, as outlined in the general introduction. Flight speeds that had been collected could then be compared statistically to the calculated V_{mp} and V_{mr}.

2.2 MATERIALS AND METHODS

Calibration of the radar gun and measurement details of flight velocity, wind velocity, morphology, and the study species and locations are outlined below. Most flights were recorded of birds returning to the nest after foraging. If the foraging site could be seen or if the birds were known to be on their way to a foraging site (*i.e.* they returned a short while later with prey) outgoing flight speeds from the nest were also included. In most cases, the nesting site was known, and if not, food was observed being carried in the bill.

1. Study Species

Flight speeds were recorded for the following seven species:

a. Tree Swallow (*Tachycineta bicolor*), Family: Hirundinidae, Order: Passeriformes

b. Mountain Bluebird (*Sialia currucoides*), Family: Turdidae, Order: Passeriformes

c. European Starling (*Sturnus vulgaris*), Family: Sturnidae, Order: Passeriformes

d. White-throated Swift (*Aeronautes saxatalis*), Family: Apodidae, Order: Apodiformes

e. Black Tern (*Chlidonias nigra*), Family: Laridae, Order: Charadriiformes

f. Pigeon Guillemot (*Cepphus columba*), Family: Alcidae, Order: Charadriiformes

g. Red-necked Grebe (*Podiceps grisegena*), Family: Podicipedidae, Order: Podicipediformes

2. Study Locations

The study locations (all in British Columbia, Figure 1), their grid reference and altitude above sea level are given below:

a. The Cotton Ranch near Riske Creek ($51° 58' N, 122° 31' W$, $1158m$).

b. Doc English Bluff - Ecological Reserve No.101 ($51° 57' N, 122° 16' W$, $610m$).

c. Williams Lake - Scout Island Nature Centre ($52° 07' N, 122° 07' W$, $590m$).

d. Mandarte Island ($48° 38' N, 125° 17' W$, $1m$).

e. Creston Valley Wildlife Management Area, Creston ($49° 06' N, 116° 31' W$, $593m$).

3. Measurement of Flight Velocity

Flight velocities were measured using a hand-held Doppler K15 radar gun (Blake *et al.*, 1989). The radar gun is able to detect small objects and the digital readout display was modified to read to $0.1 ms^{-1}$, with a range of 3 to 30 ms^{-1}. The gun was calibrated with respect to a stopwatch (LCD Professional Quartz, accurate to $\pm 0.05s$) and known distances using automobiles, motorcycles, and bicycles.

Calibrations were performed with a moving target at 0° , 10° , 20° , and 30° relative to the long axis of the radar gun. Radar speeds were corrected using the cosine correction factor (Operators Manual for Stationary Radar). Table 1 shows the results of the two sample t-test and a linear regression comparing the calculated stopwatch speed with the radar speed at each angle. For 0° ,10° , and 20° there was no significant difference between calculated stopwatch speeds and recorded radar speeds. Values at 30° were significantly different. Thus, radar speeds recorded in the range of ±20° would not be significantly different from those recorded at 0° . In most cases, it was possible to point the radar gun directly (±10°) into the bird flight path. It was noted during the calibration that at angles of 30° and greater, recordings from bicycles were not detected. This suggests that birds in this range would also be undetected and this was confirmed in the field measurements.

4. Flight Speed Recordings for Each Species

a. Tree Swallow (*Tachycineta bicolor*),and Mountain Bluebird (*Sialia currucoides*)

Both of these species nested in nestboxes on the Cotton Ranch near Riske Creek, B.C.. The nextboxes were mounted on fenceposts along the fencelines which separate the

FIGURE 1. Map of Study Locations

The five locations - Williams Lake, Riske Creek, Ecological Reserve No.101, Mandarte Island, and the Creston Valley Wildlife Management Area - where bird flight speeds were taken are plotted, as well as two reference points - Prince George and Vancouver.

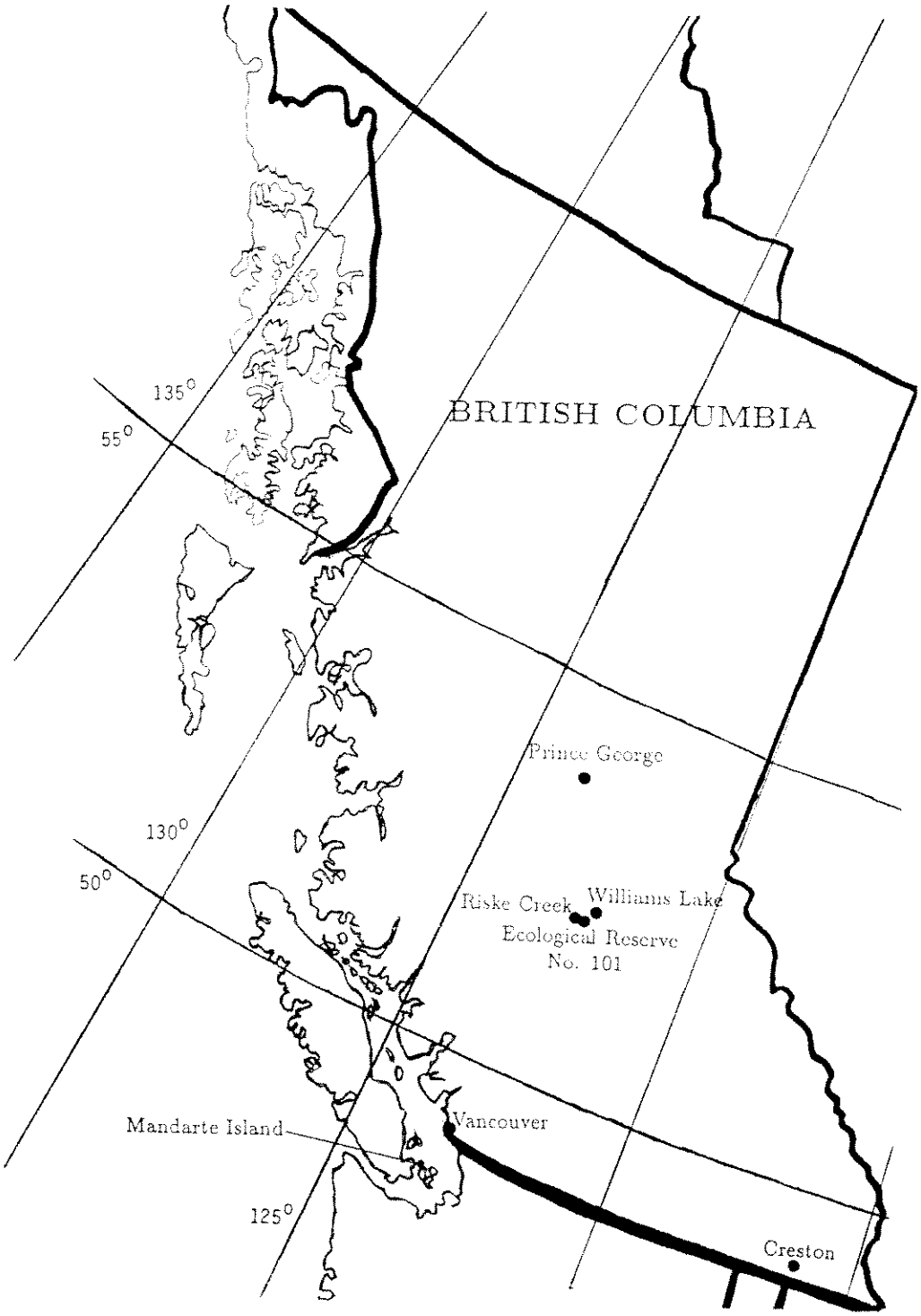

BRITISH COLUMBIA
135°
55°
130°
50°
125°
Prince George
Riske Creek
Williams Lake
Ecological Reserve
No. 101
Mandarte Island
Vancouver
Creston

TABLE I. RADAR CALIBRATION

H_o : **Radar speed = Stopwatch speed**

Angle	**Two Sample T-Test** $\alpha = .05, n = 25$	**Linear Regression** Radar vs. Stopwatch
0°	$p = 0.8480$	$r^2 = 94.45\%$
10°	$p = 0.9828$	$r^2 = 88.58\%$
20°	$p = 0.9189$	$r^2 = 97.93\%$
30°	$p = 0.0065$	$r^2 = 95.06\%$

fields. Much of the terrain was flat and treeless so the activities of the birds were easily observed from a distance. Nesting records were kept for 16 bluebird nests and 13 swallow nests. Flight speed records were attempted for most nesting pairs initially, but many of the bluebirds appeared upset at the disturbance and either abandoned the nest temporarily until I left or visited the nest very infrequently and cautiously. At five bluebird nests, however, my presence caused little or no disturbance and the parents freely flew to and from the nest. Mountain Bluebird flight speeds were thus based on ten individuals - five females and five males, with a total of 263 flight speeds. Flight speed records for the Tree Swallows also represent five females and five males, totalling 313 recordings.

The radar gun was positioned, in each case, far enough away from the nest so as not to distress the parents, yet close enough to detect the majority of incoming and outgoing flights. This distance was approximately $5 - 10m$ from the nest, depending on the birds. Since the radar gun was usually capable of displaying two or three readouts before the bird was out of range, it could be determined if the bird was accelerating or decelerating. Flights where readouts varied by more than 10% were disregarded.

Flight speeds were recorded on a daily basis between May 25 and June 17, 1988 for the Mountain Bluebirds and from June 12 to June 18, 1988 for the Tree Swallows. No measurements were taken on days when the wind speed was measured to be greater than $0.5ms^{-1}$. In order to decrease the variability in flight speed recordings between birds due to the time of day, recordings were collected as close as possible to the same time period each day at each nest. Thus, although the timing of the flight recordings will vary between nests, it is fairly constant within each nest. Recordings and observations were made usually for one hour per nest each day for the bluebirds and one half hour per nest each day for the swallows.

b. White-throated Swift (*Aeronautes saxatalis*)

Flight speed records for this species were obtained on June 12, June 14, and June 17, 1988 at Doc English Bluff - a cliff overlooking the Fraser River. Velocities were determined for approximately 15 individuals, with a total of 104 speeds. Flight velocities

were recorded for wind velocities for up to $0.5ms^{-1}$, and during stronger winds, flight velocity measurements were not taken.

c. European Starling (*Sturnus vulgaris*)

European Starling flight velocities were recorded on three consecutive days (June 9-11, 1988) at five different nests at the Scout Island Nature Centre in Williams Lake. The nests were located in holes in trees, and all flight records represent only flights of parents returning to the nest. The total number of speeds measured was 163, from ten individuals. Male and female velocities were not analysed separately.

d. Pigeon Guillemot (*Cepphus columba*)

Measurements of this species, totalling 230 flight speeds of approximately 80 individuals, were obtained on Mandarte Island over a two-day period (June 21 and June 22, 1988). Velocities were recorded from the shore as the birds left and returned to the rock cliffs in which they nest. Although the Pigeon Guillemot may fly near enough to the water surface to be considered as using the ground effect, the velocities measured were of birds out of the ground effect. In some cases, velocities were recorded of birds just beginning to ascend to the cliffs or near the end of their descent from the cliffs. Because no eggs or young were actually observed in the visible rock crevices, and it was early in the season, the birds may not have begun to feed their young. Thus, the flights observed may have been just feeding flights for the parents themselves. Male and female flight speeds were not analysed separately.

e. Red-necked Grebe (*Podiceps grisegena*)

Flight velocities for the Red-necked grebe were obtained as the birds flew over a dyke between a lake and marshy area, at the Creston Valley Wildlife Management Area near Creston (June 25 and June 26, 1988). The birds were observed on their return flight from foraging as they flew along the lake, and small fish could be seen between their bills.

In total, 64 speeds were collected, and again, male and female speeds were not analysed separately.

f. Black Tern (*Chlidonias nigra*)

The 41 flight velocities obtained for the Black Tern were recorded by Clive Welham of Simon Fraser University on July 2, July 11, and July 17, 1988. Speeds were measured at the Creston Valley Wildlife Management Area, while birds were flying to and from a specific known foraging site.

5. Measurement of Wind Velocity

An anemometer (Anemo, West Germany), accurate to $\pm 0.5 ms^{-1}$, was used to measure wind velocity. Flight speeds were recorded mainly on days when the measured wind velocity was less than $0.5 ms^{-1}$. The anemometer was positioned as close as possible to the height of the flight speed path, which was usually only $1 - 3m$ above the recording position.

6. Morphological Measurements

Morphological measurements (Table II) obtained include those required to construct aerodynamic power versus flight velocity curves (body mass, M, wingspan, b, wing area, S_w, body diameter, d) as well as measurements for comparative purposes (aspect ratio, AR $(= b^2/S_w)$, wingloading, Q $(= M/S_w)$). Values for some species were determined from measurements of the actual study specimens in the field while others were taken from specimens in the Burke Museum at the University of Washington and the Vertebrate Museum at the University of British Columbia. Literature sources (Poole, 1938; Savile, 1957; Bartholomew *et al.*, 1957; Hartman, 1961; Drent, 1965; Bedard, 1969; Dunning, 1984; Rayner, 1985*b*) were also used.

Field measurements of mass (M) were determined using a $50g$ spring balance. Wing span (b) and body diameter (d) were measured with a $1m$ measuring tape. Tracings of wings were made, which were later digitized to determine wing area. Figure 2 shows wing tracings drawn to scale and the aspect ratios of each of the seven study spcies.

TABLE II. MORPHOLOGICAL MEASUREMENTS

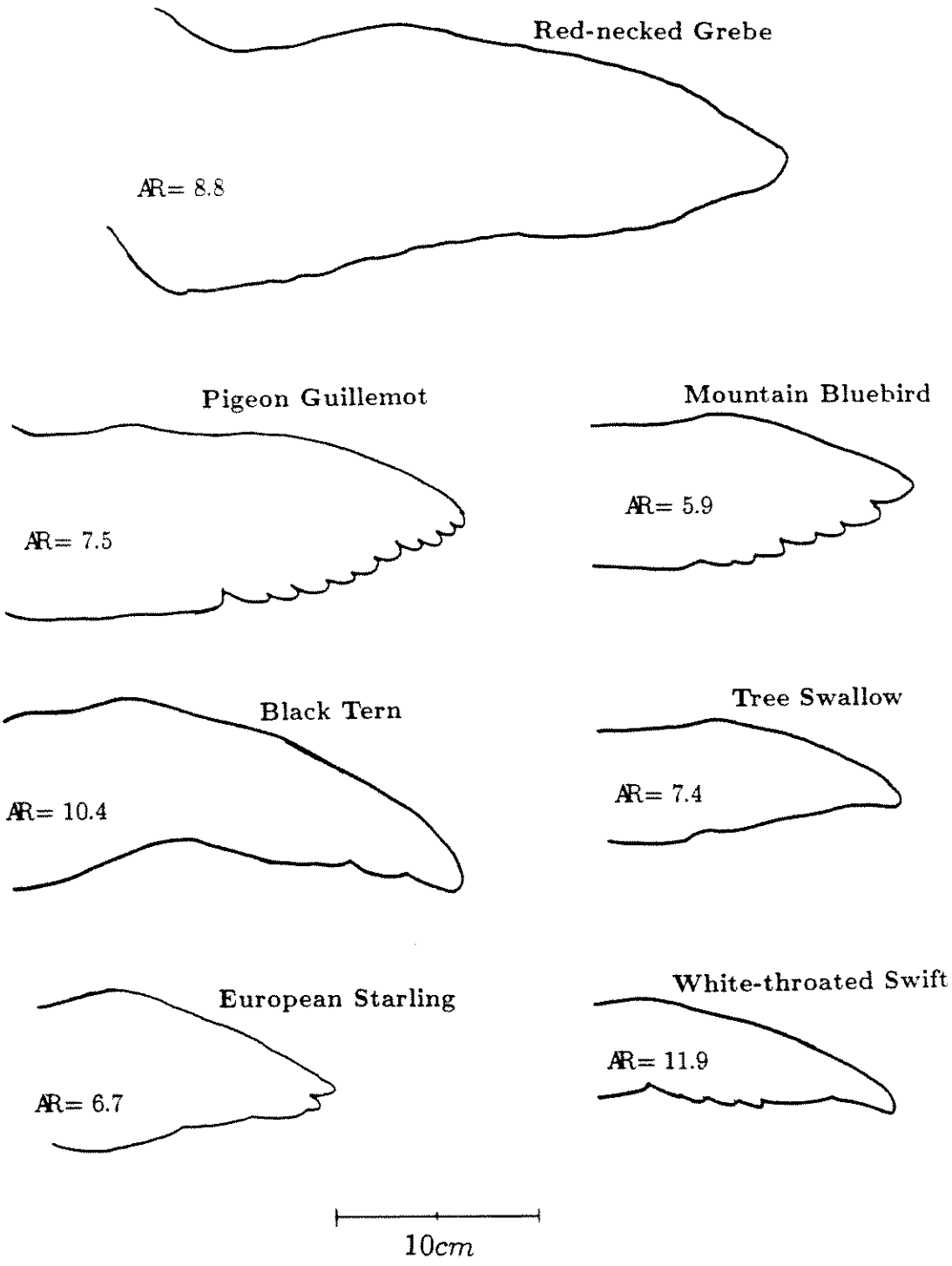
Species	Mass (kg),n	b (m),n	S_w (m^2),n	Q $(N \cdot m^{-2})$,n	AR b^2/S_w
Tree Swallow	$.020, 82^a$				
	$.020, 1^b$		$.0125, 1^b$	$15.8, 1^b$	
	$.017, 5^c$	$.298, 10^{c,d}$	$.012, 10^{c,d}$	$13.9, 5^{c,d}$	$7.4^{c,d}$
Mountain Bluebird	$.028, 16^a$				
	$.0285, 11^c$	$.309, 12^{c,d}$	$.0163, 12^{c,d}$	$17.2, 11^{c,d}$	$5.9^{c,d}$
White-throated Swift	$.0325, 20^a$				
	$.0305, 19^e$	$.326, 3^{c,d}$	$.0089, 3^{c,d}$		$11.9^{c,d}$
Black Tern	$.065, 36^a$				
	$.060^f$	$.557^f$	$.035^f$	16.8^f	8.9^f
	$.053, 5^c$	$.535, 5^{c,d}$	$.0275, 5^{c,d}$	$19.1, 5^{c,d}$	$10.4^{c,d}$
European Starling	$.0799, 915^a$				
	$.0847, 1942^a$				
	$.084, 3^b$		$.019, 3^b$	$43.4, 3^b$	
	$.08 - .09, 11^g$	$.344, 4^d$	$.0176, 4^d$		6.7^d
	$.076^h$	$.389^h$	$.021^h$	36.6^h	7.2^h
Pigeon Guillemot	$.487, 5^a$	$.508, 12^d$	$.0343, 12^d$	$128.7^{j,d}$	7.5^d
	$.483, 6^i$				
	$.450, 53^j$				
Red-necked Grebe	$1.023, 6^a$	$.725, 5^d$	$.0598, 5^d$	$167.8^{a,d}$	8.8^d

SOURCES:

a. Dunning, 1984
b. Poole, 1938
c. Field Measurements, 1989
d. Burke Museum, 1989
e. Bartholomew, 1957
f. Savile, 1957
g. Hartman, 1961
h. Rayner, 1985
i. Bedard, 1969
j. Drent, 1965

FIGURE 2. Wing Shapes and Aspect Ratios

Wing outlines traced from actual wings and drawn to scale for the seven study species are shown. As well, aspect ratios ($AR = b^2/S_w$) are listed for each species for comparative purposes.


Red-necked Grebe
AR= 8.8
Pigeon Guillemot
AR= 7.5
Mountain Bluebird
AR= 5.9
Black Tern
AR= 10.4
Tree Swallow
AR= 7.4
European Starling
AR= 6.7
White-throated Swift
AR= 11.9
10cm

7. Power Curve Input Values

Table III gives the input values necessary for the plotting of aerodynamic power versus velocity for each each species. Values were also used from Table II. Field morphology measurements obtained from this study and museum specimen measurements were preferred over literature values. $C_{D(pro)}$, $C_{D(para)}$, A_p, and P_{met} were determined as described in the general introduction for each species. The air density, ρ, was determined based on the altitude at each of the study locations. A range of values for the European Starling was used because of the variance in reported morphological measurements.

TABLE III. POWER CURVE INPUT VALUES

Species	$C_{D(pro)}$	$C_{D(para)}$	ρ (kgm^{-3})	A_p (m^2)	P_{met} (W)
Tree Swallow	0.02	0.40	1.11	7.069×10^{-4}	0.075
Mountain Bluebird	0.02	0.40	1.11	8.867×10^{-4}	0.109
White-throated Swift	0.02	0.40	1.16	8.023×10^{-4}	0.071
European Starling	0.02	0.40	1.16	1.459×10^{-3} 1.558×10^{-3}	0.222 0.239
Black Tern	0.02	0.40	1.16	1.148×10^{-3}	0.104
Pigeon Guillemot	0.02	0.35	1.23	4.774×10^{-3}	0.489
Red-necked Grebe	0.02	0.30	1.16	8.254×10^{-3}	0.886

2.3 RESULTS

The results of flight speed measurements are presented in Table IV. The total number of flight speeds recorded is 1178, and distributions of the data for each species are shown in Figure 3. The column showing the results of a χ^2 fit to a normal distribution (Table IV) shows that, for five of the seven species, the flight speeds recorded were not normally distributed, indicating that nonparametric statistics should be employed in any further analyses. However, parametric statistics, especially the t-test, are generally quite robust, particularly when using large and/or equal sample sizes (*e.g.* see Zar, 1984). In addition, the power of the t-test is actually greater when the populations have leptokurtic distributions. When using the Mann-Whitney-U test, for example, any comparison samples larger than $n_1 = 20$ and $n_2 = 40$ have a critical U value determined by the t-test critical t at $t_{\alpha,(1),\infty}$ (Zar, 1984). Since the data sets that are not normally distributed are leptokurtic, and because the sample sizes are relatively large, parametric statistics are employed.

Based on measurements from Tables II and III, plots of aerodynamic power required for flight versus flight velocity were constructed for each species (Figures 4 - 10). The minimum power speed, V_{mp} and the maximum range speed, V_{mr}, are defined on each curve, and represent the predicted optimal flight speeds based on the minimum cost of flight per unit time or minimum cost of flight per unit distance respectively. The slowest velocity on the curve represents V_{stall}. The mean of the actual flight speeds recorded with the radar gun V_{obs}, is also shown on each species' power curve, as well as the maximum power, P_{max}, available to the birds for flight. For the European Starling, because of the wide range of masses reported, two power curves were constructed based on minimum and maximum values of mass, with their corresponding maximum range speed, minimum power speed, maximum power and maximum velocity defined. Boxplots outline the distribution of speeds for each species.

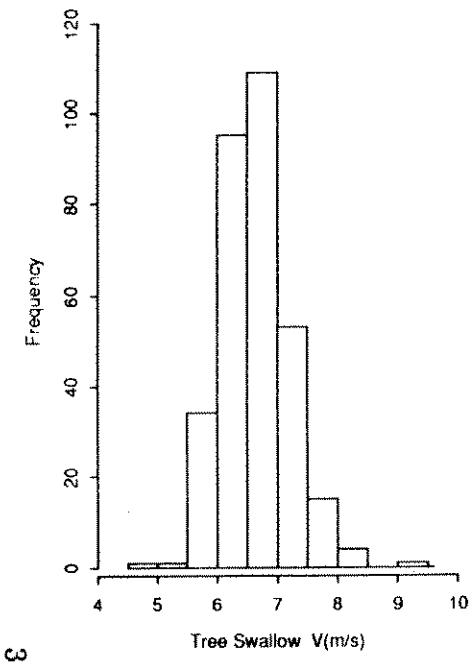
Table V expresses numerically V_{obs}, V_{mp}, and V_{mr}, and compares the observed speeds with V_{mp} and V_{mr} separately using a One-Sample T-test. Two sets of morphological measurements were used as power curve inputs for the European Starling, represented by

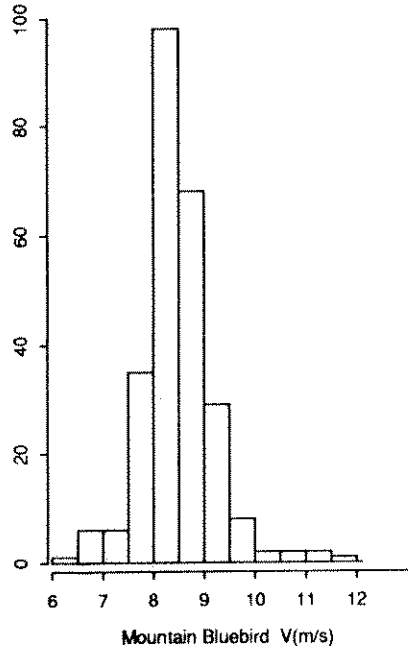
TABLE IV. RESULTS OF FLIGHT SPEED MEASUREMENTS

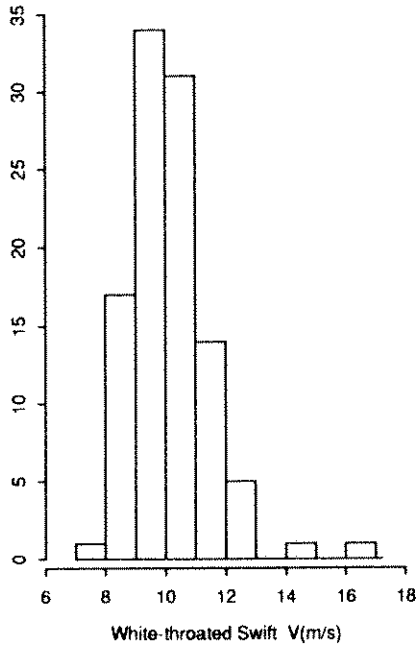
Species	n	**Mean ± s.e.** ms^{-1}	**Range** ms^{-1}	χ^2 **Fit to normal distribution**
Tree Swallow	313	6.6 ± 0.03	$4.8 - 9.0$	$p = 0.003$
Mountain Bluebird	263	8.4 ± 0.04	$6.2 - 11.9$	$p < 0.001$
White-throated Swift	104	10.1 ± 0.1	$7.1 - 16.5$	$p = 0.06$
European Starling	163	9.8 ± 0.04	$8.8 - 10.9$	$p = 0.015$
Black Tern	41	7.1 ± 0.1	$5.1 - 9.5$	$p = 0.02$
Pigeon Guillemot	230	10.5 ± 0.08	$8.3 - 14.2$	$p < 0.001$
Red-necked Grebe	64	10.7 ± 0.09	$8.9 - 12.2$	$p = 0.72$

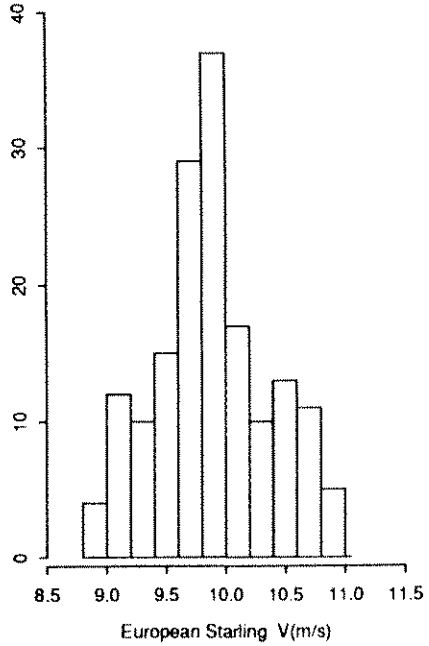
FIGURE 3. Flight Speed Frequency Histograms

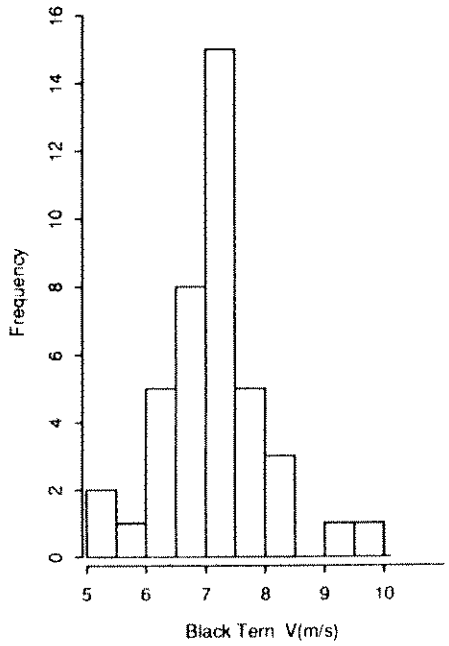
Frequency histograms for each species are plotted. Summary statistics and information on each distribution can be found in Table V.

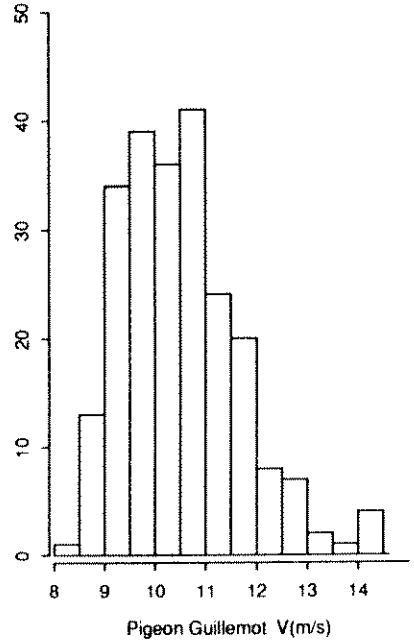

Frequency
Tree Swallow V(m/s)


Mountain Bluebird V(m/s)


White-throated Swift V(m/s)


European Starling V(m/s)


Frequency
Black Tern V(m/s)


Pigeon Guillemot V(m/s)

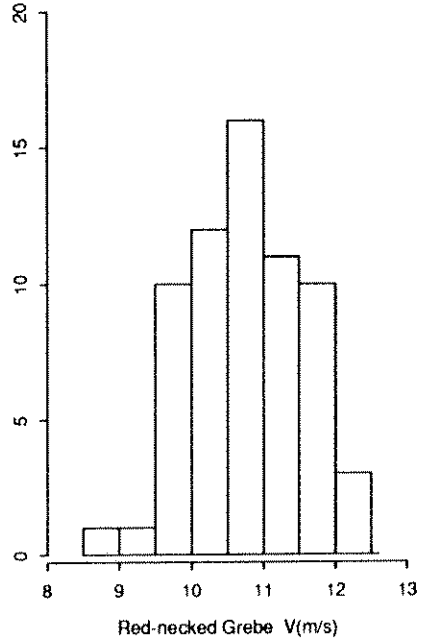

Red-necked Grebe V(m/s)

FIGURE 4. Tree Swallow Power Curve

Power (W) required for flight is plotted against flight velocity (ms^{-1}) for the Tree Swallow. The minimum power speed, V_{mp}, maximum range speed, V_{mr}, and the observed speed, V_{obs} are shown, as is a boxplot of the flight speed distribution. The box covers the upper and lower quartiles, with the central line as the median. The horizontal lines show the range of the data, with extreme values plotted as points. P_{max} is the maximum power available to the flight muscles at $250Wkg^{-1}$, and V_{max} the corresponding maximum flight speed possible.

FIGURE 5. Mountain Bluebird Power Curve

Power (W) required for flight is plotted against flight velocity (ms^{-1}) for the Mountain Bluebird. The minimum power speed, V_{mp}, maximum range speed, V_{mr}, and the observed speed, V_{obs} are shown, as is a boxplot of the flight speed distribution. The box covers the upper and lower quartiles, with the central line as the median. The horizontal lines show the range of the data, with extreme values plotted as points. P_{max} is the maximum power available to the flight muscles at $250Wkg^{-1}$, and V_{max} the corresponding maximum flight speed possible.

FIGURE 6. White-throated Swift Power Curve

Power (W) required for flight is plotted against flight velocity (ms^{-1}) for the White-throated Swift. The minimum power speed, V_{mp}, maximum range speed, V_{mr}, and the observed speed, V_{obs} are shown, as is a boxplot of the flight speed distribution. The box covers the upper and lower quartiles, with the central line as the median. The horizontal lines show the range of the data, with extreme values plotted as points. P_{max} is the maximum power available to the flight muscles at $250Wkg^{-1}$, and V_{max} the corresponding maximum flight speed possible.

FIGURE 7. European Starling Power Curve

Power (W) required for flight is plotted against flight velocity (ms^{-1}) for the European Starling. The minimum power speed, V_{mp}, maximum range speed, V_{mr}, and the observed speed, V_{obs} are shown, as is a boxplot of the flight speed distribution. The box covers the upper and lower quartiles, with the central line as the median. The horizontal lines show the range of the data, with extreme values plotted as points. A second power curve is plotted using greater morphological values, resulting in $V_{mp}\prime$, and $V_{mr}\prime$. P_{max} and $P_{max}\prime$ are the maximum power available to the flight muscles at $250Wkg^{-1}$ for the ranges in mass used, and V_{max} and $V_{max}\prime$ the corresponding maximum flight speeds possible.

FIGURE 8. Black Tern Power Curve

Power (W) required for flight is plotted against flight velocity (ms^{-1}) for the Black Tern. The minimum power speed, V_{mp}, maximum range speed, V_{mr}, and the observed speed, V_{obs} are shown, as is a boxplot of the flight speed distribution. The box covers the upper and lower quartiles, with the central line as the median. The horizontal lines show the range of the data, with extreme values plotted as points. P_{max} is the maximum power available to the flight muscles at $250Wkg^{-1}$, and V_{max} the corresponding maximum flight speed possible.

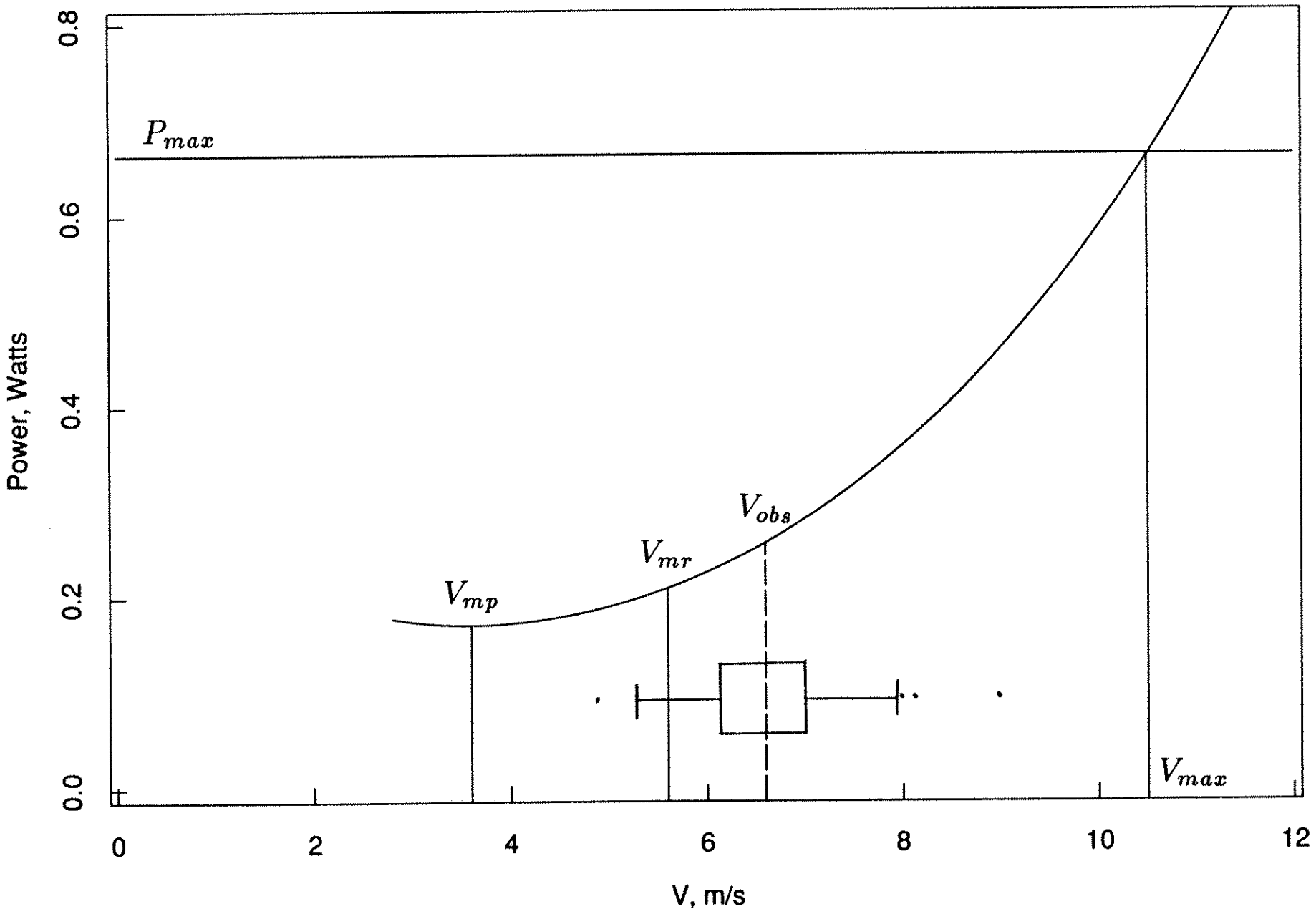
FIGURE 9. Pigeon Guillemot Power Curve

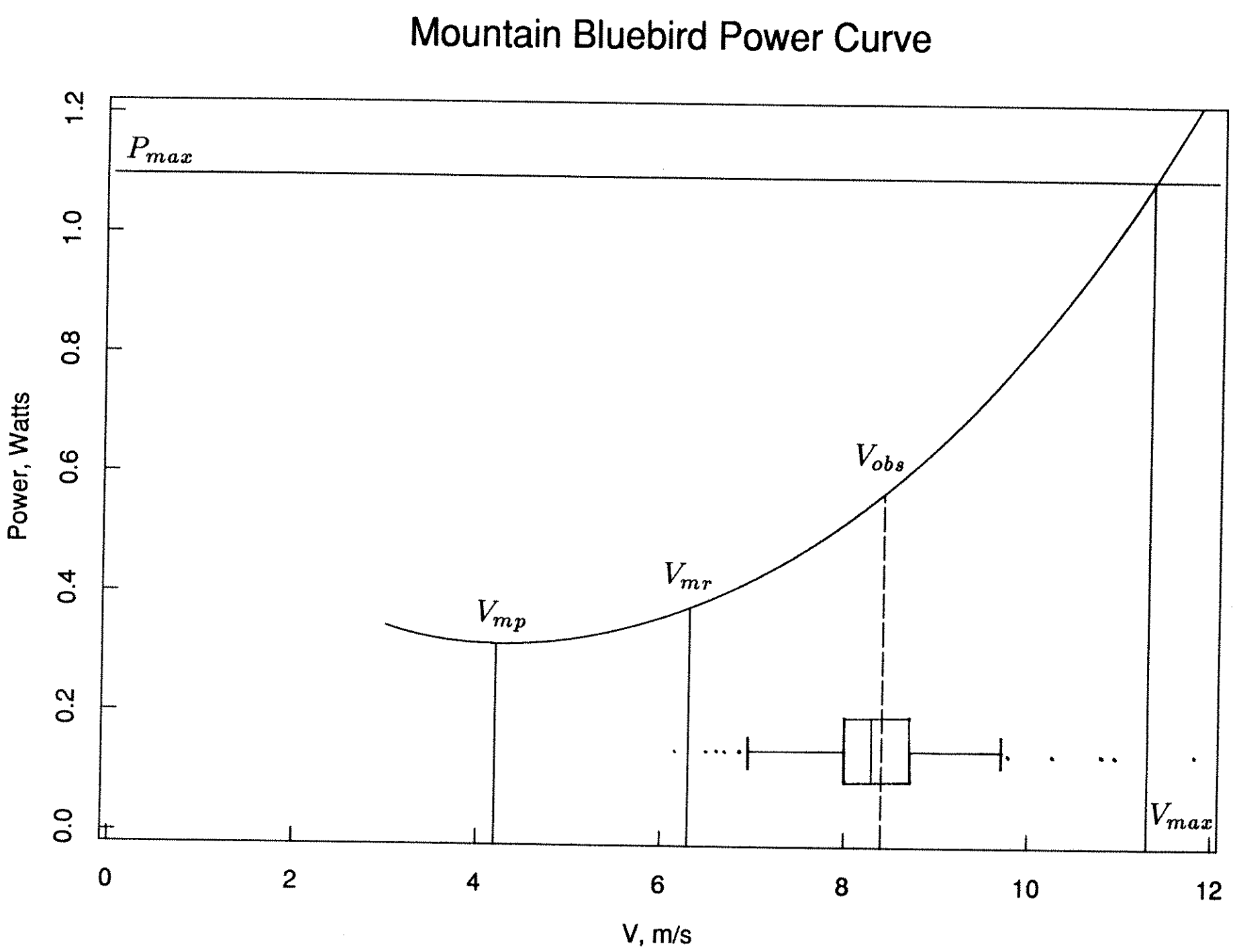
Power (W) required for flight is plotted against flight velocity (ms^{-1}) for the Pigeon Guillemot. The minimum power speed, V_{mp}, maximum range speed, V_{mr}, and the observed speed, V_{obs} are shown, as is a boxplot of the flight speed distribution. The box covers the upper and lower quartiles, with the central line as the median. The horizontal lines show the range of the data, with extreme values plotted as points. P_{max} is the maximum power available to the flight muscles at $250Wkg^{-1}$, and V_{max} the corresponding maximum flight speed possible.

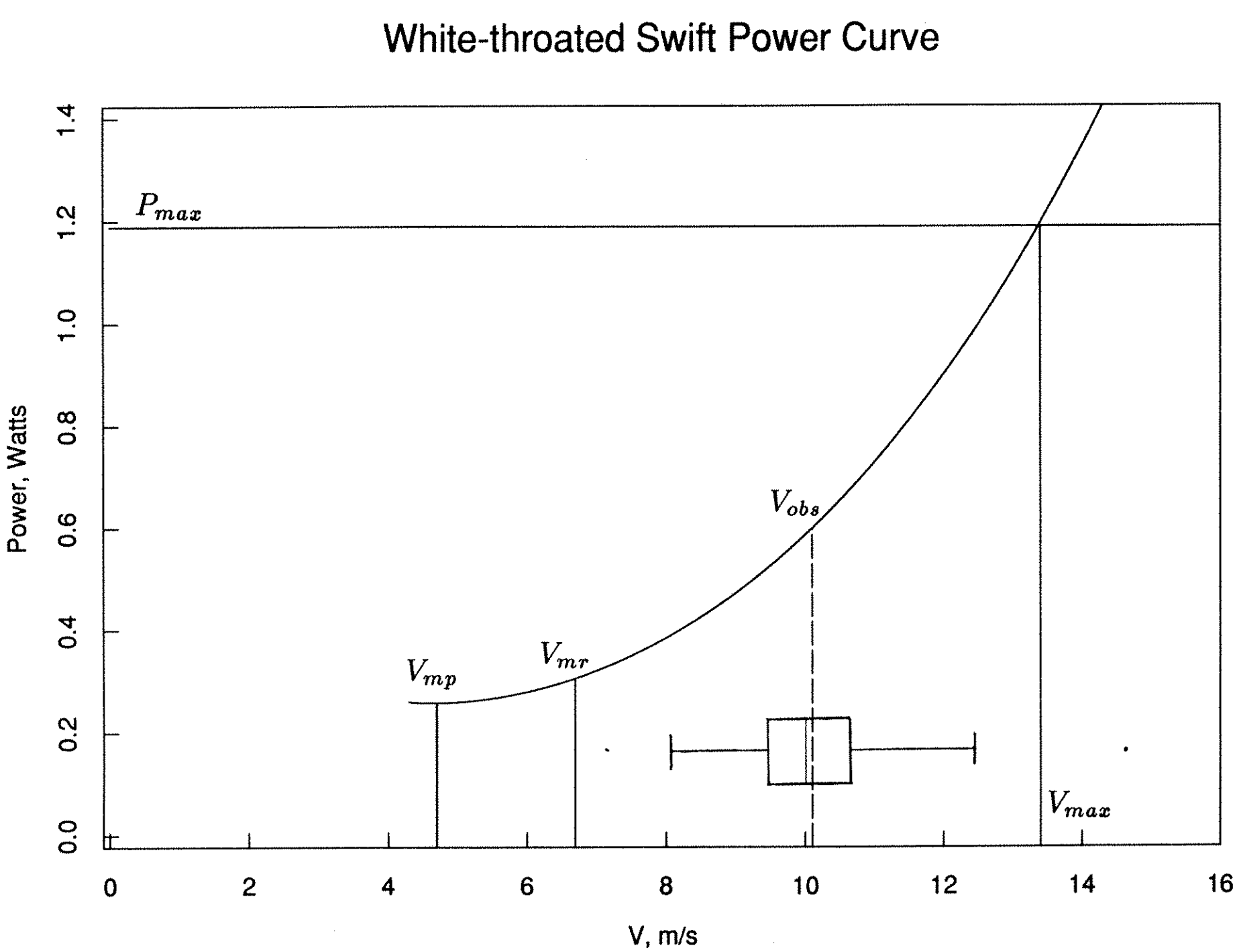
FIGRUE 10. Red-necked Grebe Power Curve

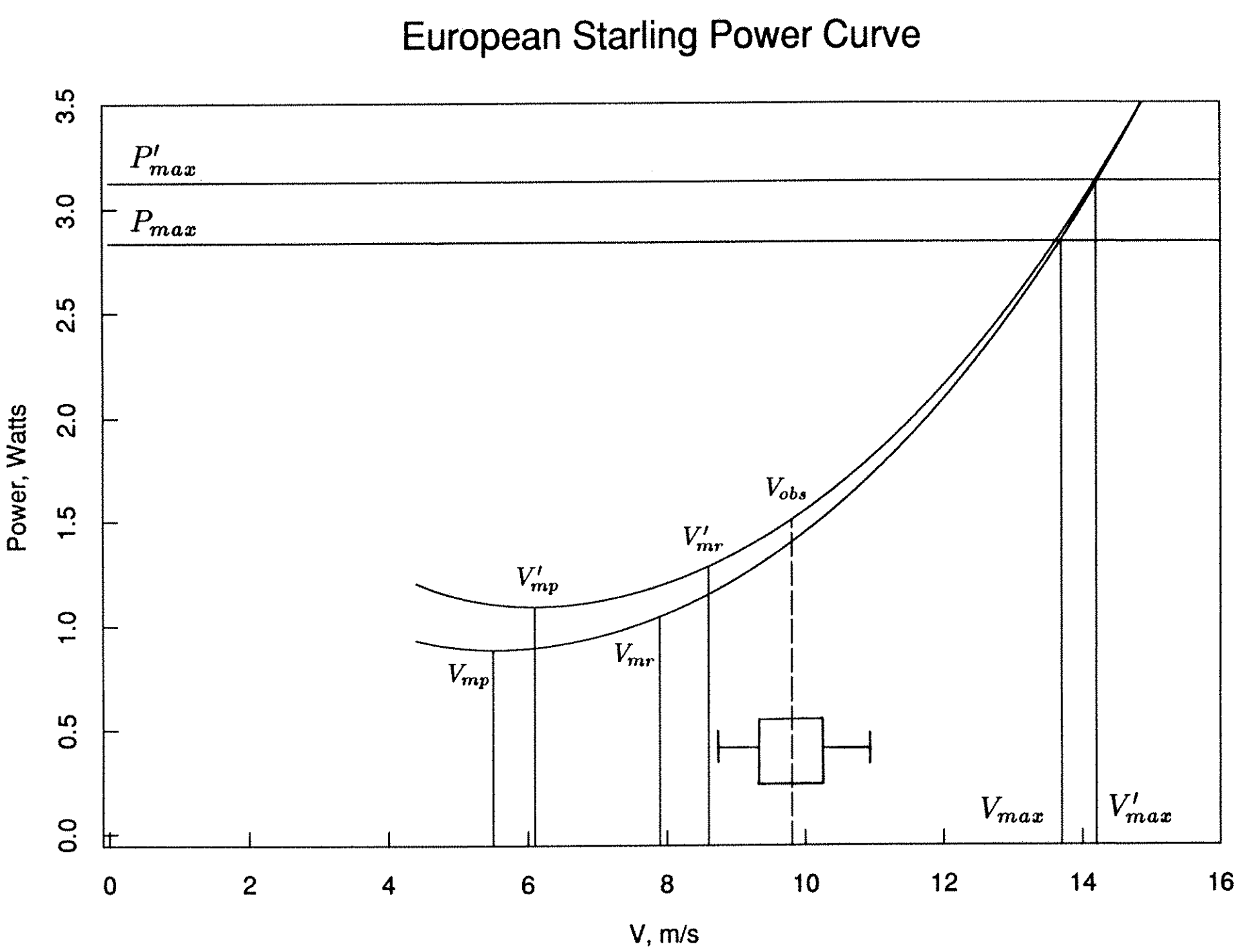
Power (W) required for flight is plotted against flight velocity (ms^{-1}) for the Red-necked Grebe. The minimum power speed, V_{mp}, maximum range speed, V_{mr}, and the observed speed, V_{obs} are shown, as is a boxplot of the flight speed distribution. The box covers the upper and lower quartiles, with the central line as the median. The horizontal lines show the range of the data, with extreme values plotted as points. P_{max} is the maximum power available to the flight muscles at $250Wkg^{-1}$, and V_{max} the corresponding maximum flight speed possible.

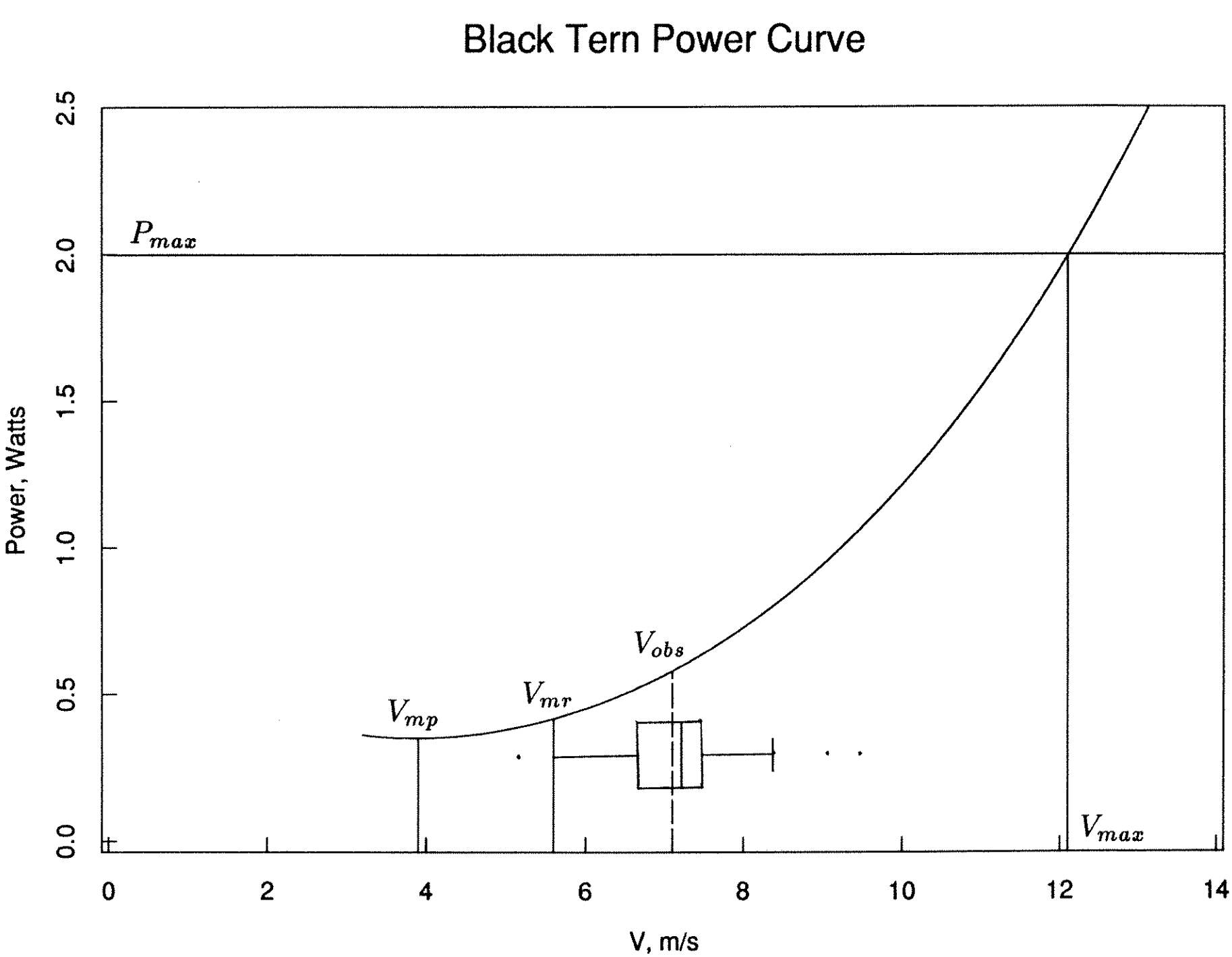
Tree Swallow Power Curve

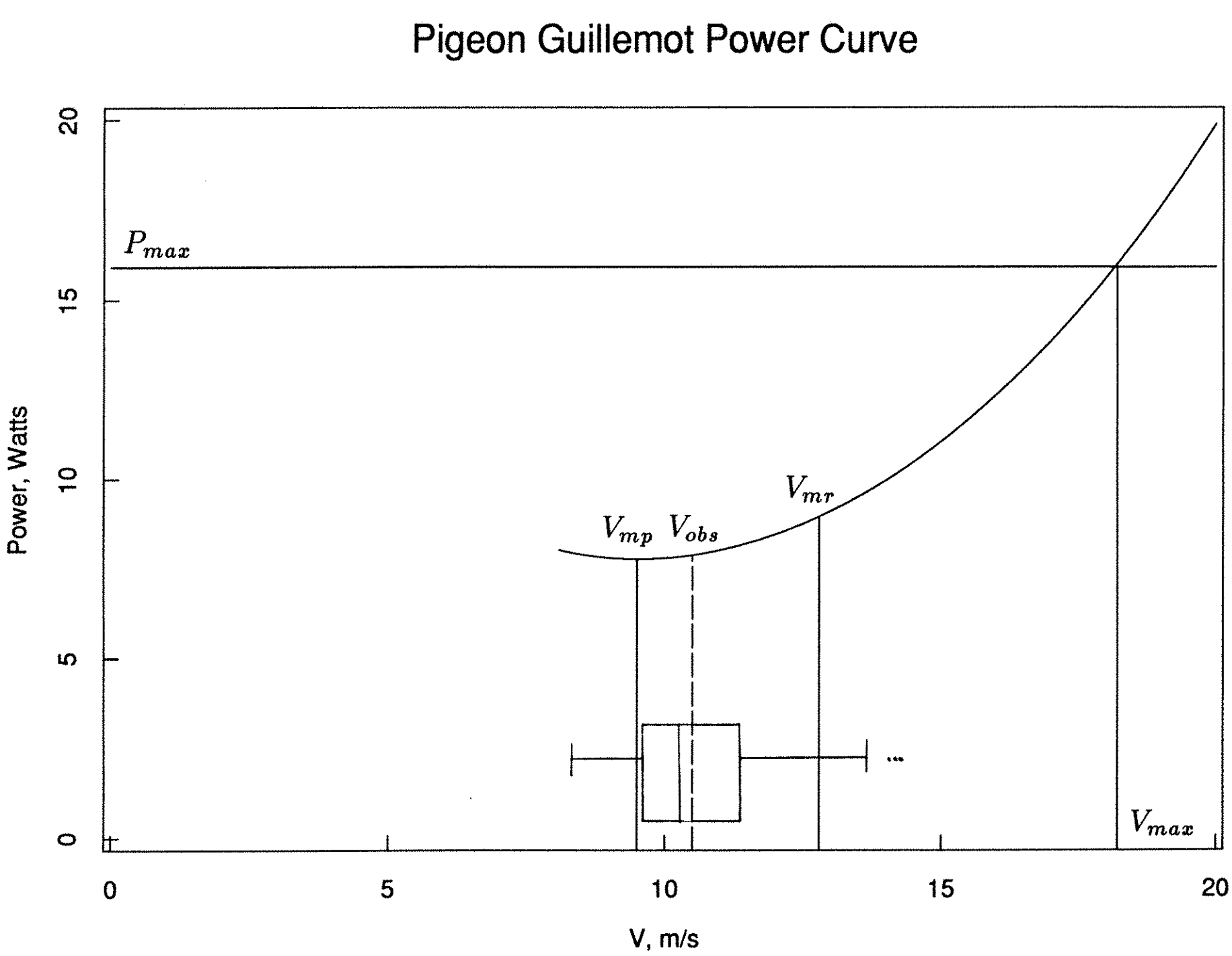


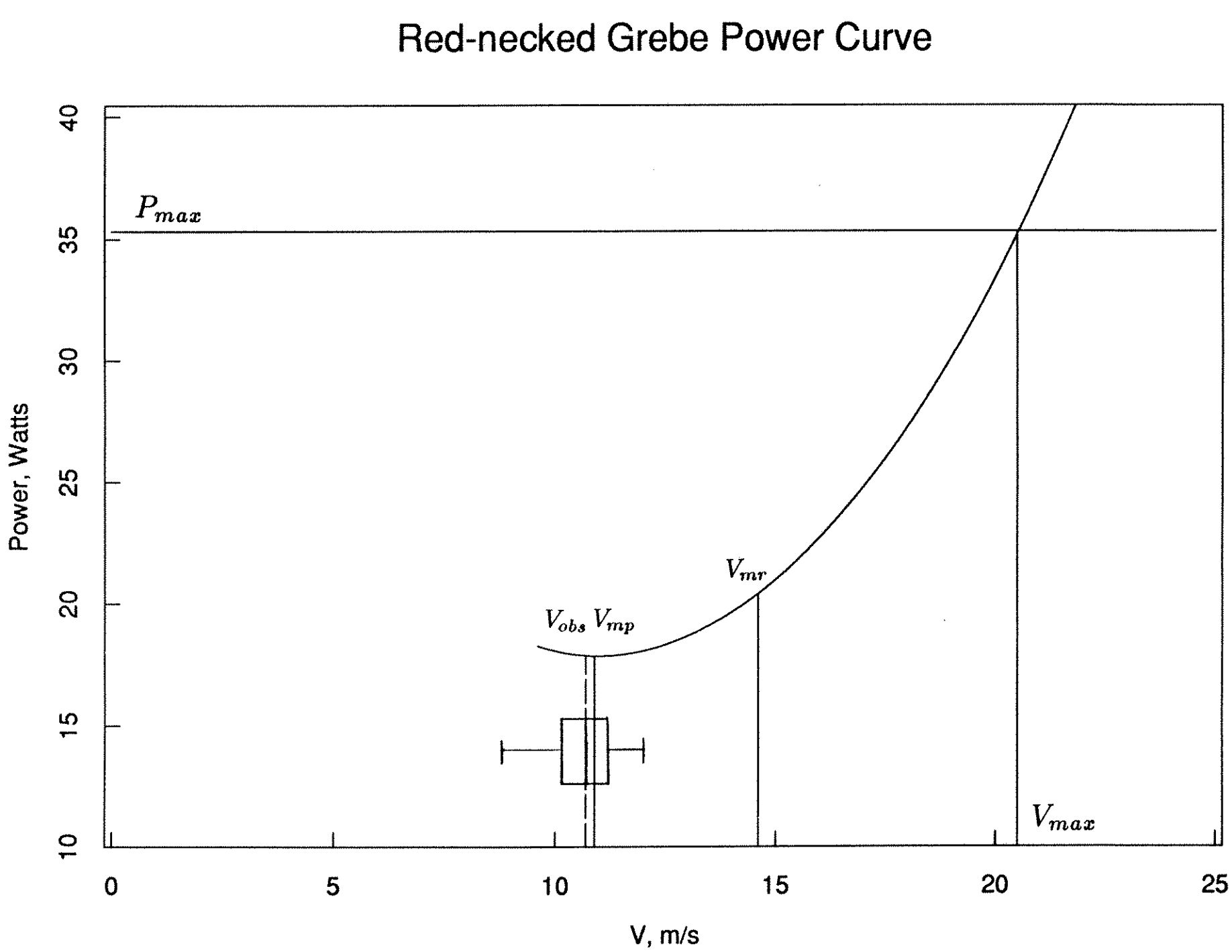

Mountain Bluebird Power Curve
Power, Watts
V, m/s
P_{max}
V_{mp}
V_{mr}
V_{obs}
V_{max}
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0
2
4
6
8
10
12


White-throated Swift Power Curve
Power, Watts
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
P_{max}
V_{obs}
V_{mr}
V_{mp}
V_{max}
0
2
4
6
8
10
12
14
16
V, m/s


European Starling Power Curve
Power, Watts
V, m/s
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
2
4
6
8
10
12
14
16
P'_{max}
P_{max}
V_{obs}
V'_{mr}
V'_{mp}
V_{mr}
V_{mp}
V_{max}
V'_{max}


Black Tern Power Curve
Power, Watts
V, m/s
P_{max}
V_{mp}
V_{mr}
V_{obs}
V_{max}
0.0
0.5
1.0
1.5
2.0
2.5
0
2
4
6
8
10
12
14


Pigeon Guillemot Power Curve
Power, Watts
V, m/s
0
5
10
15
20
P_{max}
V_{mp}
V_{obs}
V_{mr}
V_{max}


Red-necked Grebe Power Curve
Power, Watts
10
15
20
25
30
35
40
P_{max}
V_{mr}
V_{obs} V_{mp}
V_{max}
0
5
10
15
20
25
V, m/s

masses of $0.076kg$ and $0.084kg$ with their corresponding wing spans and wing areas. Two values, then, for each of V_{mp} and V_{mr} are reported. At the significance level of 0.05, all of the observed speeds were significantly different from both V_{mp} and V_{mr}. For the Tree Swallow, Mountain Bluebird, White-throated Swift, and Black Tern, V_{obs} was greater than V_{mp} and V_{mr}, while V_{obs} for the Pigeon Guillemot was situated between the two predicted optimal speeds. V_{obs} for the Red-necked Grebe was less than V_{mp}.

To test the robustness of the power curve and thus the results of comparisons between observed and predicted speeds, the drag coefficients $C_{D(para)}$ and $C_{D(pro)}$ were each reduced until the null hypothesis $H_o : V_{obs} = V_{mr}$ was not rejected (Table VI). The second column of Table VI describes the proportion of the original estimate of $C_{D(para)}$ required for V_{obs} to be insignificantly different from V_{mr} for each species. In most cases, as well as a 99% reduction in $C_{D(para)}$, it was also necessary to reduce $C_{D(pro)}$. The third column represents the values of $C_{D(pro)}$ needed to meet the above requirements. An increase in either drag coefficient would reduce the values of V_{mp} and V_{mr}, and thus result in even greater discrepancies between observed and predicted speeds.

The flight speed data were collected at different nesting sites if possible, or, alternatively, on different days using the same group of individuals. Data for Mountain Bluebirds, Tree Swallows and European Starlings were collected at five separate nests for each species, with each nest representing speeds from both the male and female. For the Black Terns, White-throated Swifts, Red-necked Grebes, and Pigeon Guillemots, flight velocities were measured on different days for the same group of birds. Table VII describes the sample size of each group, the mean, standard error, and range of speeds. The last column indicates the results of a one factor analysis of variance or a t-test performed for each species between the groupings of data. There was no difference between speed recording groups for the Mountain Bluebirds, European Starlings, Black Terns, and the Red-necked Grebes. Tree Swallows, White-throated Swifts and Pigeon Guillemots were significantly different with respect to their data groupings. Table VIII describes the results of a Tukey test performed for the species which showed differences between groups.

TABLE V. COMPARISON OF OBSERVED AND PREDICTED SPEEDS

Species	V_{obs} (ms^{-1})	V_{mp} (ms^{-1})	V_{mr} (ms^{-1})	V_{max} (ms^{-1})	H_o : $V_{obs} = V_{mp}$	H_o : $V_{obs} = V_{mr}$
Tree Swallow	6.6	3.6	5.6	13.7	$p < 0.001$	$p < 0.001$
Mountain Bluebird	8.4	4.2	6.3	11.3	$p < 0.001$	$p < 0.001$
White-throated Swift	10.1	4.7	6.7	13.4	$p < 0.001$	$p < 0.001$
European Starling	9.8	5.5	7.9	13.7	$p < 0.001$	$p < 0.001$
	9.8	6.1	8.6	14.2	$p < 0.001$	$p < 0.001$
Black Tern	7.1	3.9	5.6	12.1	$p < 0.001$	$p < 0.001$
Pigeon Guillemot	10.5	9.5	12.8	18.2	$p < 0.001$	$p < 0.001$*
Red-necked Grebe	10.7	10.9	14.6	20.5	$p = 0.03$**	$p < 0.001$*

* $V_{obs} < V_{mr}$

** $V_{obs} < V_{mp}$

TABLE VI. VALUES OF $C_{D(para)}$ AND $C_{D(pro)}$ REQUIRED TO ACCEPT THE NULL HYPOTHESIS

$$H_o : V_{obs} = V_{mr}, \quad \alpha = 0.05 \tag{1}$$

Species	$C_{D(para)}$	$C_{D(pro)}$
Tree Swallow	$0.01C_{D(para)} + 0.85C_{D(pro)}$	$0.30C_{D(pro)}$
Mountain Bluebird	$0.01C_{D(para)} + 0.55C_{D(pro)}$	$0.05C_{D(pro)}$
White-throated Swift	$0.01C_{D(para)} + 0.44C_{D(pro)}$	$0.01C_{D(pro)} + 0.50C_{D(para)}$
European Starling	$0.01C_{D(para)} + 0.75C_{D(pro)}$ $0.10C_{D(para)}$	$0.08C_{D(pro)}$ $0.30C_{D(pro)}$
Black Tern	$0.01C_{D(para)} + 0.68C_{D(pro)}$	$0.27C_{D(pro)}$

TABLE VII. SUMMARY STATISTICS FOR MEASUREMENT GROUPS AND ONE-WAY ANOVA BETWEEN GROUPS

H_o : No difference between groups or nests

Group	n	Number of Nestlings	$V_{obs} \pm s.e.$ ms^{-1}	Range ms^{-1}	ANOVA
Bluebird nests					
1	38	6, 1	8.3 ± 0.1	$6.9 - 9.7$	
2	57	4	8.5 ± 0.09	$7.5 - 10.9$	
3	78	4	8.3 ± 0.06	$6.7 - 9.2$	$p = 0.1980$
4	24	4	8.5 ± 0.1	$7.2 - 10.1$	
5	66	4	8.4 ± 0.1	$6.2 - 11.9$	
Swallow nests					
1	95	6	6.7 ± 0.06	$5.6 - 9.0$	
2	49	5	6.6 ± 0.07	$5.3 - 7.9$	
3	70	6	6.6 ± 0.07	$5.5 - 8.0$	$p = 0.0179$
4	49	5	6.6 ± 0.07	$4.8 - 7.3$	
5	50	5	6.4 ± 0.07	$5.8 - 8.0$	
Starling nests					
1	30		9.8 ± 0.09	$8.8 - 10.9$	
2	30		9.7 ± 0.09	$9.0 - 10.7$	
3	32		9.9 ± 0.08	$8.9 - 10.8$	$p = 0.3346$
4	35		9.9 ± 0.09	$9.0 - 10.9$	
5	36		9.9 ± 0.07	$8.9 - 10.8$	
Tern groups					
1	17		7.0 ± 0.2	$5.1 - 7.9$	
2	12		7.2 ± 0.2	$6.3 - 9.1$	$p = 0.7776$
3	12		7.1 ± 0.3	$5.1 - 9.5$	
Swift groups					
1	23		11.3 ± 0.2	$8.5 - 16.5$	
2	17		9.3 ± 0.3	$7.1 - 11.5$	$p < 0.001$
3	64		9.9 ± 0.1	$8.5 - 11.5$	
Grebe groups					
1	43		10.7 ± 0.1	$8.9 - 12.2$	
2	21		10.6 ± 0.2	$9.0 - 12.0$	$p = 0.5969$
Guillemot groups					
1	24		9.8 ± 0.2	$8.7 - 12.2$	
2	25		9.8 ± 0.2	$8.8 - 12.7$	
3	108		10.7 ± 0.1	$9.0 - 13.5$	$p < 0.001$
4	73		10.6 ± 0.2	$8.3 - 14.2$	

TABLE VIII. TUKEY TEST RESULTS FOR
TREE SWALLOW, WHITE-THROATED SWIFT
PIGEON GUILLEMOT

Species	Homogeneous Groups	
Tree Swallow		
Nest 1	*	
Nest 2	*	*
Nest 3	*	*
Nest 4	*	*
Nest 5		*
White-throated Swift		
Group 1	*	
Group 2		*
Group 3		*
Pigeon Guillemot		
Group 1	*	
Group 2	*	
Group 3		*
Group 4		*

For the Mountain Bluebird and Tree Swallow, a two-factor analysis of variance was performed to determine whether the sexes flew at different speeds or whether incoming and outgoing foraging flights were different. Table IX shows that there is no significant difference in speeds using either condition for each of the two species. A Mann-Whitney test was employed to detect a possible difference in flight speeds in Black Terns leaving the nest and returning to the nest, but no difference was found (Table X).

Since there may have been some variance in flight speeds depending on the time of day of the recording, in cases where measurements were made on more than two or three consecutive days, the time periods of the recordings were kept as constant as possible for each nest. Thus, for the Mountain Bluebird and Tree Swallow, the exact time in terms of day, hour, and minute is known for each flight speed recorded. The flight speed data are plotted with respect to the time of day for the Mountain Bluebird (Figure 13) and Tree Swallow (Figure 14). A regression through each plot resulted in a slope of 0.014 for the Mountain Bluebird and a slope of 0.018 for the Tree Swallow. Neither slope was significantly different from zero ($p > 0.25$ for each regression).

TABLE IX. TWO-WAY ANOVA TEST RESULTS FOR
MOUNTAIN BLUEBIRD, TREE SWALLOW

H_o : No difference between male and female speeds or speeds to or from a foraging site

Interaction with flight speed	**Mountain Bluebird**	**Tree Swallow**
1.male vs. female	$p = 0.40$	$p = 0.19$
2.to vs. from site	$p = 0.15$	$p = 0.40$
2-factor interaction		
1.vs 2.	$p = 0.07$	$p = 0.52$

TABLE X. MANN-WHITNEY TEST RESULT FOR BLACK TERN

H_o : No difference in flight speeds leaving or returning to the nest

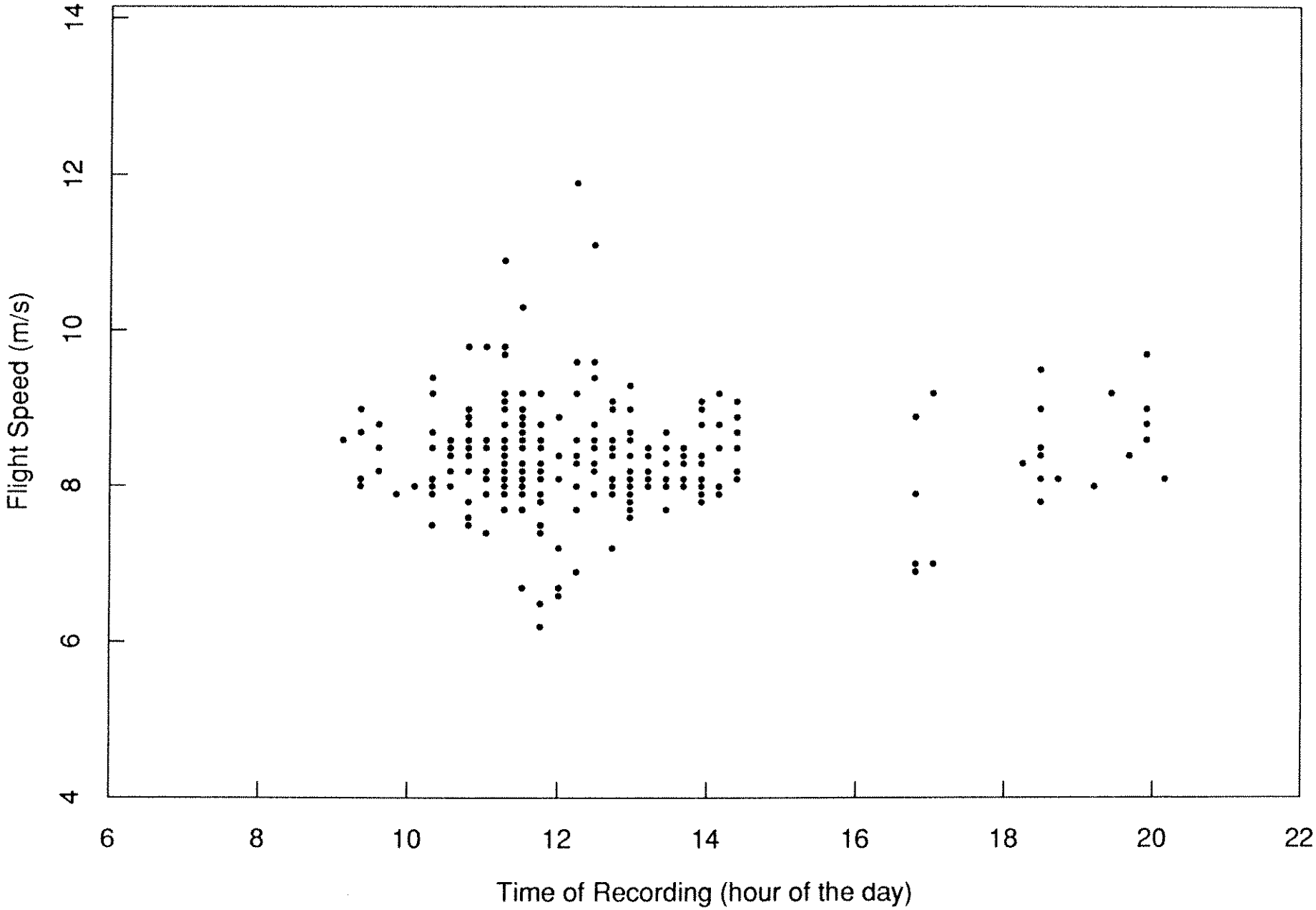
	n	V_{obs}	Mann-Whitney
Leaving nest	12	6.9	
Returning	29	7.2	$p = 0.8139$

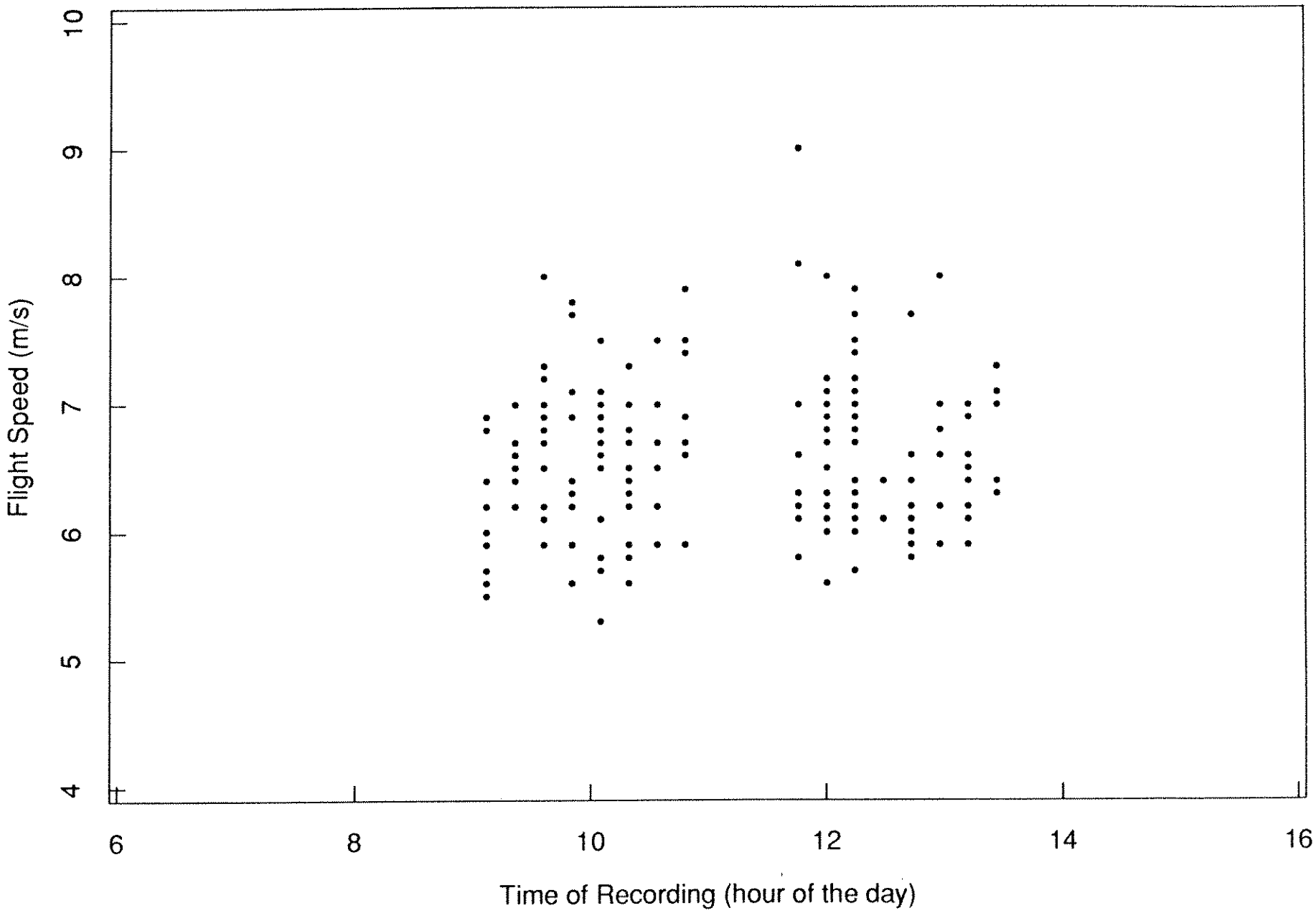
FIGURE 11. Flight Speed Versus Time of Recording For The Mountain Bluebird

Each recorded flight speed is plotted with respect to the time of the recording in hours. Plotted here are flight speeds from all Mountain Bluebird nests.

FIGURE 12. Flight Speed Versus Time of Recording For The Tree Swallow

Each recorded flight speed is plotted with respect to the time of the recording in hours. Plotted here are flight speeds from all Tree Swallow nests.


Flight Speed (m/s)
4
6
8
10
12
14
6
8
10
12
14
16
18
20
22
Time of Recording (hour of the day)


Flight Speed (m/s)
4
5
6
7
8
9
10
6
8
10
12
14
16
Time of Recording (hour of the day)

2.4 DISCUSSION

Results of comparisons of observed velocities with predicted minimum power and maximum range speeds indicate that in five of seven species the observed velocity is significantly greater than both V_{mp} and V_{mr} (Table V, Figures 4 - 10). For the Pigeon Guillemot, however, the observed speed lies between the minimum power and maximum range speeds while V_{obs} for the Red-necked Grebe is actually less than the theoretical V_{mp}. All speeds, with the exception of a few by the Mountain Bluebird, are within the maximum sustainable velocity predicted using $250 W kg^{-1}$ of flight muscle (Weis-Fogh and Alexander, 1977).

In order to change the results of comparisons between V_{mr} and V_{obs} for the Tree Swallow, Mountain Bluebird, White-throated Swift, European Starling, and Black Tern, vastly different values for the drag coefficients $C_{D(para)}$ and $C_{D(pro)}$ were necessary (Table VI). To shift the power curve such that the value of V_{mr} would not be significantly different from V_{obs}, for the White-throated Swift, for example, values of 0.004 for $C_{D(para)}$ and 0.009 for $C_{D(pro)}$ would have to be used, instead of the originally estimated values of 0.4 and 0.02 respectively. Even the smallest deviation from original estimates, which occurred in the cases of the Tree Swallow and the greater set of values for the European Starling, involves using only 30% of the original value for $C_{D(pro)}$. The above comparisons suggest, then, that the power curve constructed for each species and the statistical comparisons made between predicted and observed velocities are quite robust. The Pigeon Guillemot and the Red-necked Grebe were not included in this sensitivity analysis because their mean observed flight speeds were already significantly less than V_{mr}. Altering $C_{D(para)}$ and $C_{D(pro)}$ for these two species would bascially shift the power curve such that V_{obs} would be situated in varying positions between V_{mp} and V_{mr}.

The χ^2 fit to a normal distribution for each species (Table IV) indicates that only the White-throated Swift and Red-necked Grebe have normally distributed speeds. The other distributions (Figure 3) indicate a clumping around the mean, and can be described as leptokurtic. This indicates that there was a stronger preference for certain velocities

near the mean than is predicted for a normal distribution. If a particular flight speed was important to maximize efficiency under certain conditions, then such a distribution would be expected.

Table XII lists previously recorded speeds from other sources for the study species. Measurements made using techniques other than doppler radar cannot realistically be considered comparable. Radar measurements noted by Rayner (1985*b*) for the starling of $9-10ms^{-1}$ are similar to the mean found in this study. Schnell and Hellack (1979) reported a mean of $10.7ms^{-1}$ for starlings ($n = 8$). Schnell and Hellack (1979) also recorded 33 flight speeds for the Black Tern in windless conditions with a mean of $7.9ms^{-1}$, close to the $7.1ms^{-1}$ mean determined in this study. Although the above mentioned speeds are similar to ones found in this study, the context of the flight behaviour is not given.

Flight speeds for each species were measured either at separate nests over a given period or with groups of birds over a given period. Table VII shows that between Bluebird nests, Starling nests, Tern groups and Grebe groups there were no bird flight speed differences. There were, however, differences in flight speeds between Swallow nests, Swift groups, and Guillemot groups. The sources of the differences are shown in Table VIII. Differences between nest one and five for the Tree Swallow may just be due to individual variation of the adults, since all other conditions were similar for all nests. Data for the White-throated Swift were collected on three separate days, represented by Groups 1, 2, and 3. All were measured using the same group of individuals in the early evening of each day, but neither number of young or nestling age could be determined. Even if the speeds had been divided into two groups, with groups 2 and 3 separated from group 1, the results of comparisong with V_{mr} would be the same, since the predicted V_{mr} was only $6.7ms^{-1}$. Flight speeds of the Pigeon Guillemot were collected over a two day period, in the morning and afternoon of each day. Groups 1 and 2 represent speeds for the afternoon flights while Groups 3 and 4 are speeds of morning flights.

There was no difference in flight speed for either male or female Mountain Bluebirds or Tree Swallows or between birds leaving and returning to the nest (Table IX, Figures 11,

TABLE XI. PREVIOUSLY RECORDED FLIGHT SPEEDS

Species	n	Flight Velocity (ms^{-1})	Method	Source
Tree Swallow	1	11.2	speedometer	Meinertzhagen,1955
Mountain Bluebird	1	8.0	speedometer	Cottam *et al.*,1942
Sialia sp.	2	7.6	speedometer	Cooke,1933
	4	5.8 – 11.6	speedometer	Meinertzhagen,1955
European Starling		9.0 – 10.0	doppler radar	Rayner,1985
		8.0 – 18,0	wind tunnel	Torre-Bueno and Larochelle,1978
	8	10.7	doppler radar	Schnell and Hellack,1979
	3	11.6 – 14.3	speedometer	Meinertzhagen,1955
	17	10.3 – 14.3	speedometer	"
	22	20.1 – 21.7	theodolite	"
	13	19.2 – 21.9	stopwatch	"
	3	20.6		"
	3	18.3 – 21.5	speedometer	"
		> 20.1	speedometer	"
	7	21.5 – 22.5	stopwatch	"
	4	12.5 – 24.6	speedometer	"
	7	11.2 – 13.6		"
Black Tern	2	9.4,10.3	speedometer	Cottam *et al.*,1942
	1	4.5	speedometer	Cottam *et al.*,1942
	33	7.9	doppler radar	Schnell and Hellack,1979

12). Black Terns leaving and returning to the nest also showed no significant difference in flight speed, although the sample size for leaving the nest was small ($n = 12$).

Since the actual time in terms of day, hour, and minute was recorded for most bluebird and swallow flight measurements, a plot of flight speed versus the time (in hours) was done to check for any variation of flight speed with time of recording (Figures 11, 12). There appears to be no variation in flight speed with time of day, indicating that for the Mountain Bluebird and the Tree Swallow, the mean speeds of the $8.4ms^{-1}$ and $6.6ms^{-1}$ respectively are representative of the flight speed at the times of the day under observation.

CHAPTER THREE

DETAILED OBSERVATIONS OF TWO SPECIES

3.1 INTRODUCTION

Many mathematical models have been constructed to explain or describe the foraging behaviours and strategies of animals. A review of optimal foraging by Pyke *et al.* (1977) classified four main categories of optimal foraging theory - optimal diet choices, optimal patch choices, optimal time durations in particular patches, and optimal patterns and speeds of movements. Stephens and Krebs (1986) detailed extensively the construction and testing of optimal foraging models. Pyke (1981) stated that at least five suggested optimality criteria have been used to predict travel speeds of animals. These include maximizing net rate of energy gain, maximizing the ratio of net rate of energy gain to the rate of energy expenditure (growth efficiency), maximizing the ratio of growth efficiency to the rate of energy expended, maximizing distance travelled per unit energy expended (minimizing energy expended per unit distance), and minimizing metabolic rate during travel (maximimzing travel time per unit energy expended).

Norberg (1981) developed a model to predict the optimal flight speed of the adult bird when feeding its young. Flights are assumed to be only between foraging sites and the nest, with no foraging during travel. He proposed that adult birds feeding their young should actually fly faster than the maximum range speed, in order to spend more time foraging and thus bring more food to the nest. It may be argued that as a bird flies faster to its foraging site, the time spent in the air will diminish, and thus travelling flight will make up proportionately less time of the total foraging trip (and perhaps become less important as a result). However, because of the U shape of the power curve, a bird should always fly at the smallest ratio of P/V to minimize the cost per unit distance, and thus the flight speed is independent of time spent foraging.

The optimal speed, V_{opt}, predicted by Norberg lies between the maximum range velocity and the maximum speed physiologically possible by the bird. Norberg assumed that the rate of net energy gain will remain constant for a given food availability and independent of flight speed, and also that the amount of food carried on each trip does not change significantly.

The derivation of Norberg's model involves two strategies. A bird can either fly at a particular speed, termed V_o, or it can increase its speed by δv to $V_o + \delta v$. If V_o is assumed to be V_{mr}, then decreasing V_o by δv will not be a realistic option, since not only will the bird be flying at a slower velocity and have less time for foraging, but it will also require more energy per unit distance flown.

If T is the total time spent in both flying to and from the foraging site plus the actual time spent foraging, then

$$T = t_{air} + t_{for} \tag{15}$$

where t_{air} is the time spent airborne and t_{for} the time spent foraging.

In strategy one, it is assumed that the power needed to fly at V_o is P_o, and that the net rate of energy gain during foraging is P_{gain}. The difference in energy gained from foraging and energy expended in flight can be expressed as

$$\Delta E_1 = P_{gain} t_{for} - P_{air} t_{air} \tag{16}$$

Since

$$t_{air} = \frac{D}{V_o} \tag{17}$$

where D is the distance flown and V_o the flight speed, and

$$t_{for} = T - t_{air} \tag{18}$$

substitutions can be made to give

$$\Delta E_1 = P_{gain}(T - \frac{D}{V_o}) - P_o\frac{D}{V_o} \tag{19}$$

In the second strategy, the chosen flight speed is $V_o + \delta v$, with a corresponding $P_o + \delta p$ required to fly at that speed. The difference between energy gained during foraging and that spent flying at $V_o + \delta v$ is

$$\Delta E_2 = P_{gain}t_{for} - (P_o + \delta p)t_{air} \tag{20}$$

Substituting $T - t_{air}$ for t_{for} and $\frac{D}{V_o+\delta v}$ for t_{air} results in

$$. \Delta E_2 = P_{gain}(T - \frac{D}{V_o + \delta v}) - (P_o + \delta p)(\frac{D}{V_o + \delta v}) \tag{21}$$

In comparing the two strategies, if flying at $V_o + \delta v$ is a better choice than V_o, then ΔE_1 should be less than ΔE_2.

$$[P_{gain}(T - \frac{D}{V_o}) - P_o\frac{D}{V_o}] < [P_{gain}(T - \frac{D}{V_o + \delta v}) - (P_o + \delta p)(\frac{D}{V_o + \delta v})] \tag{22}$$

This simplifies to

$$\frac{P_o + \delta p}{V_o + \delta v} - \frac{P_o}{V_o} < (\frac{1}{V_o} - \frac{1}{V_o + \delta v})P_{gain} \tag{23}$$

which is the expression in Norberg (1981). If this inequality holds true, then parents feeding their young should fly at $V_o + \delta v$ $(= V_{opt})$.

For the Mountain Bluebird and the Tree Swallow, information on time spent foraging by the adults, number of visits to the nests, number of nestlings, the masses of the nestlings (only for the bluebird), as well as flight speeds to foraging sites were collected. Power curves for eight individual female adults were constructed such that the female's flight speeds could be compared to her own predicted V_{mp} and V_{mr}. Possible values of P_{gain} were determined by setting V_{obs} to V_{opt} and compared to the energy requirements of the young.

3.2 MATERIALS AND METHODS

Detailed observations during the nesting period were obtained for the Tree Swallow (*Tachycineta bicolor*) and the Mountain Bluebird (*Sialia currucoides*), from May 25 to June 17, 1988 and July 3 to July 17, 1988. Brood size, nestling mass, time budgets, and input values for power curves were determined as described below.

1. Brood Size and Mass of Nestlings

Nestling age was determined by observing dates of hatching. Nests were checked each day until all eggs had hatched or were cold to the touch. Each nest box had a removable roof, which could easily be taken off to examine the nest. Thereafter, nests were checked after each session of flight speed recordings and observations, to confirm brood size or record any deaths or disappearances of the young. The nestboxes were placed in pairs along fencelines. Each pair was approximately $30 - 50m$ away from the next pair. Within a pair of boxes the distance between the two was 1 or $2m$, and in some cases both boxes were on the same fence post. In most instances, one of the two nestboxes was occupied by a Mountain Bluebird pair and the other by a Tree Swallow pair.

Since it was not certain what the effect of handling the nestlings would be on the parents or the nestlings, the masses of the Mountain Bluebird nestlings were measured using the young from the second brood (July 3 - July 17, 1988). Approximately half of the bluebird pairs had second broods, so nestling masses and brood sizes were recorded for five nests. Only clutch sizes were recorded with respect to the Tree Swallow young for their first brood, and no second Tree Swallow broods were found.

2. Time Budgets

During the half hour or hour time period per day in which flight speeds were being obtained for each bird, time and details of activities (number of visits to the nest, time spent foraging) were also noted. Observations were recorded on paper and time noted

from a running stopwatch. In addition, one bluebird nest was observed for a full day. Since hovering played an important role in the foraging activities of the bluebirds, hovering durations were timed with a stopwatch when possible. Details of consecutive hoverings were also noted on some occasions. Total observation time was $49.2h$ for Mountain Bluebirds and $15.6h$ for Tree Swallows.

3. Individual Power Curves

In some cases, flight velocities were collected from birds for which body mass, wingspan, and body diameter had been measured. This was so for five female bluebirds and three female swallows. For these birds, separate curves of aerodynamic power for flight versus flight velocity were plotted and thus actual measured flight velocities for each bird could be compared to predicted optimal flight speeds based on its own dimensions. Table XII shows the input values necessary for the construction of power curves of the five female Mountain Bluebirds and three female Tree Swallows. Table III gives the remaining needed input values which are basically constant within a particular species.

TABLE XII. INDIVIDUAL FEMALE POWER CURVE INPUT VALUES *

Bird	Mass (kg)	$b(m)$	$S_w(m^2)$	$A_p(m^2 \times 10^4)$
Bluebird 1	0.031	0.30	0.0161	7.1
Bluebird 2	0.030	0.30	0.0166	9.6
Bluebird 3	0.029	0.31	0.0146	7.1
Bluebird 4	0.030	0.32	0.0167	7.1
Bluebird 5	0.031	0.30	0.0150	9.6
Swallow 2	0.018	0.28	0.0123	7.1
Swallow 4	0.020	0.31	0.0117	7.1
Swallow 5	0.018	0.29	0.0115	7.1

* Remaining input values obtained from Table III.

3.3 RESULTS

Table XIII summarizes observations made at five Mountain Bluebird nests and five Tree Swallow nests. Details of observations for individual nests are given in the appendix (Tables A1 - A10). The average number of visits to the nest per hour by both Mountain Bluebird parents was 11 (Table XIII), ranging from 3.2 to 28.6 visits per hour. For each parent, then, the average number of visits to the nest per hour was 5.5. Power (1980) found that the average number of visits to the nest per hour by Mountain Bluebirds was 6.1 for males and 7.1 for females, with no significant difference between the two. He noted that, over the nestling period, the parents shared equally in feeding the young. The total number of observations was 240 and there was also a wide range of values from 0 visits per hour to 29.5 visits per hour (Table 6, Power, 1980). Power did not state the number of nestlings per nest for those particular observations, while in the present study four of the five nests contained four young. The other nest originally consisted of six young but after three days only one nestling remained alive. There was no apparent difference in frequency of nest visits by the parents of this nest when compared to the other four nests.

Of the 118 bluebird foraging trips for which I recorded both the time of departure and return to the nest, the average time for one foraging trip was 2.2 minutes (Table XIII). A few observations (14 visits over 30 minutes) by Grass (1970) indicated similar results, with average foraging times of 2.6 minutes per trip for a male (5 visits over 30 minutes) and 3.2 for a female (9 visits during 30 minutes). The time for a foraging trip included the time spent feeding the young as well as obtaining more food and returning, so may account for the slightly longer trip duration than I recorded.

The mean of 165 recorded visits to the nest by the Tree Swallow in this study was 15.5, with a wide range from 6.7 to 56.5. The number of visits per hour per nestling also varied greatly, from 1.3 - 9.4, with a mean of 2.8.

A plot of the age of young versus the number of visits per hour per nestling for all nests (Figure 13) has a significant slope of 0.13 (Table XIV). However, in comparing

TABLE XIII. SUMMARY OF NEST VISITS FOR THE MOUNTAIN BLUEBIRD AND TREE SWALLOW

	n	Mean $\pm s.d.$	Median	Range
Mountain Bluebird				
# Visits/hr	390 visits	11.0 ± 6.2	9.2	2.8-28.0
Visits/hr nestling		3.2 ± 1.8	2.8	0.7-7.2
Time/trip (min)	118 trips	2.2 ± 1.0	2.0	1.0-5.0
Total time foraging (min/hr)		24.2		
Tree Swallow				
# Visits/hr	165 visits	15.5 ± 12.3	11.4	6.7-56.5
Visits/hr nestling		2.8 ± 2.0	2.1	1.3-9.4
Time/trip (min)	54 trips	1.8 ± 0.8	2.0	1.0-4.0
Total time foraging (min/hr)		27.9		

results for individual nests (Figure 14), there is no distinct trend common to all nests. Nests one and three show increased feeding rates as the nestlings mature, while nests two, four and five indicate a diminishing feeding rate with increasing nestling age. The number of feedings per hour per nestling determined by Power (1966) range from 0.7 to 3.8, while in the present study, the range was 0.7 to 7.2 feedings per hour per nestling. The greater number of feedings per nestlings in the current study may be due to a smaller brood size (an average of 4 young compared to 5 and 6 young in Power (Table 4, 1966)).

Flight speeds of adult bluebirds flying on foraging trips did not change with increasing age of the young (Figure 15). The slope of the regression is 0.012 and is not significant (Table XIV). The trends observed for each nest separately can be seen in Figure 16.

The results of tests for significant differences in flight speeds between recording days within each nest are displayed in Table XV. For the Mountain Bluebird, nests one, three, and five showed a significant difference in flight speeds between recording days, while flight speeds recorded on different days for nests two and four were found not to be significantly different.

Aerodynamic power versus flight velocity was plotted for five individual female Mountain Bluebirds, since morphological measurements as well as flight speeds were obtained from them. Table XVI indicates the results of comparisons of observed flight speeds for each female with predicted V_{mp} and V_{mr} values from the females' individual power curves. In each case, the observed flight speeds were significantly greater than the predicted V_{mp} and V_{mr}.

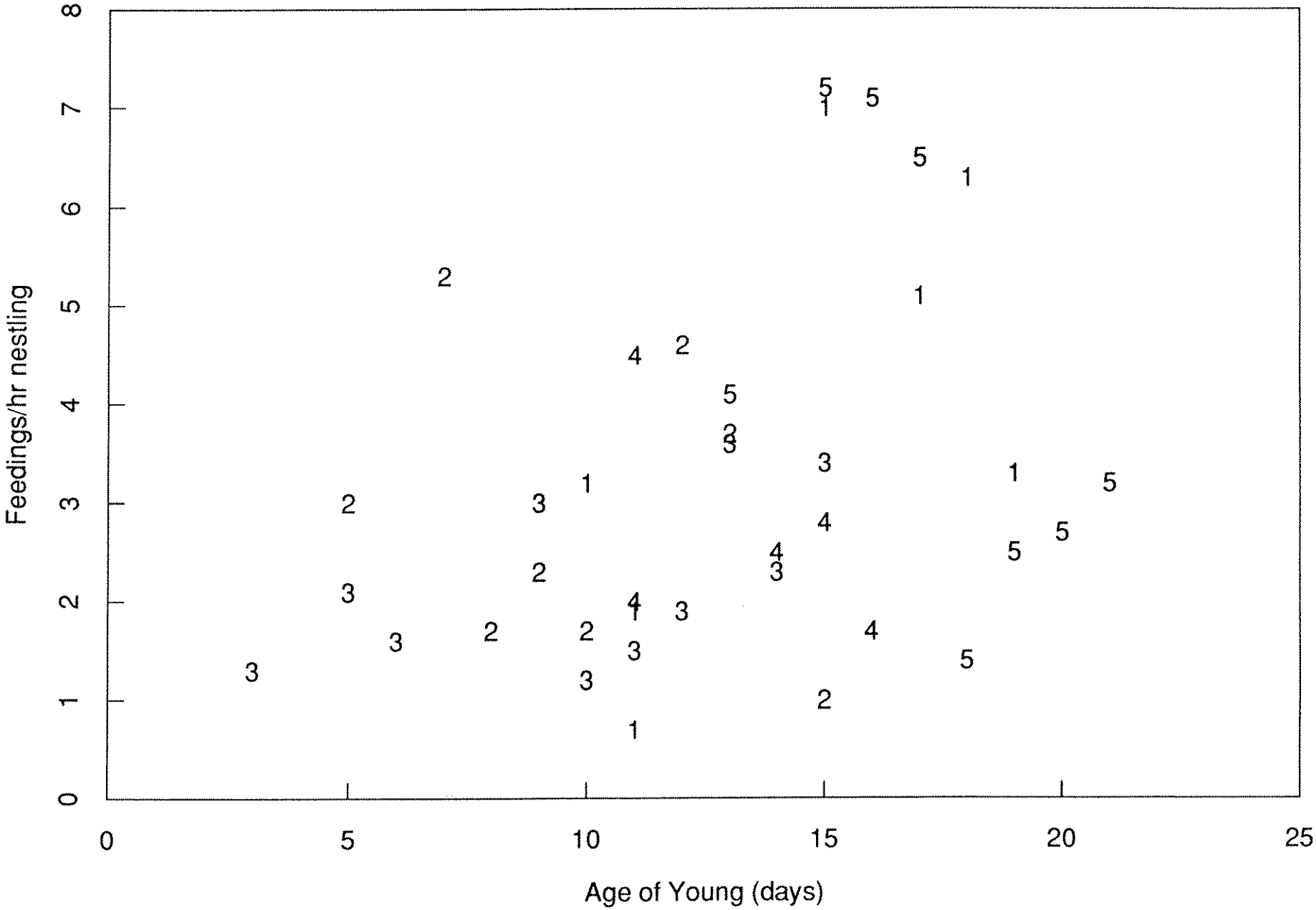
The mass of the nestlings each day was determined for the second brood of Mountain Bluebirds, at five separate nests, totalling 20 nestlings. Growth of the young is shown in Figure 17. Fitting a nonlinear regression to the plot results in a logistic growth curve, the equation of which is also defined. This growth curve is similar to one constructed using nestling data from Power (1966).

FIGURE 13. Age of Young Versus Feeding Rate For All Bluebird Nests

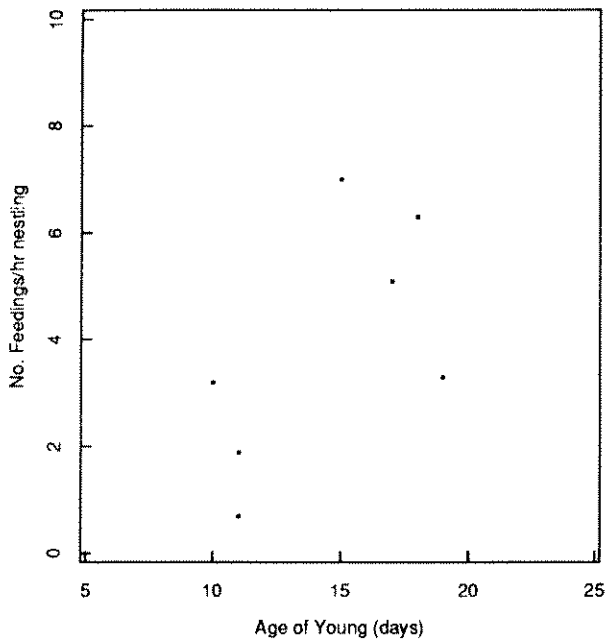
The number of feedings per hour per nestling are plotted against the age of the bluebird young. The numbers beside each point indicate from which nest the observation was made (*e.g.* 1 = Bluebird Nest One). The results of a regression through this plot are shown in Table XIV.

FIGURE 14. Age of Young Versus Feeding Rate For Individual Bluebird Nests

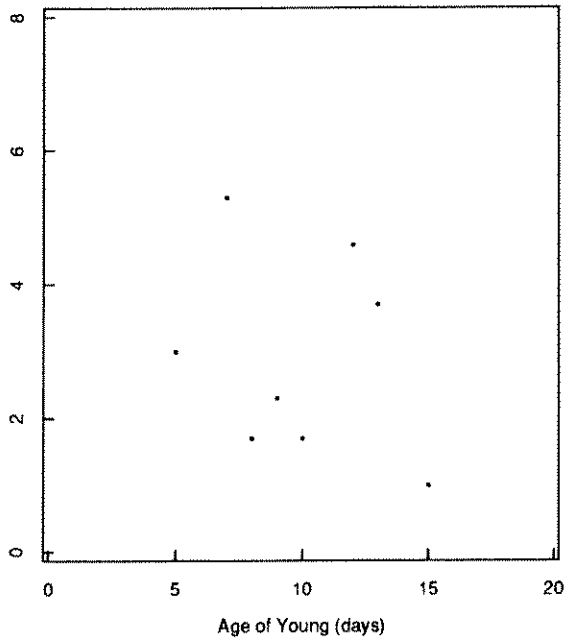
The number of feeding visits made to the nest each hour per nestling is plotted against the age of the young in days for each nest.


Feedings/hr nestling
Age of Young (days)
0
1
2
3
4
5
6
7
8
0
5
10
15
20
25

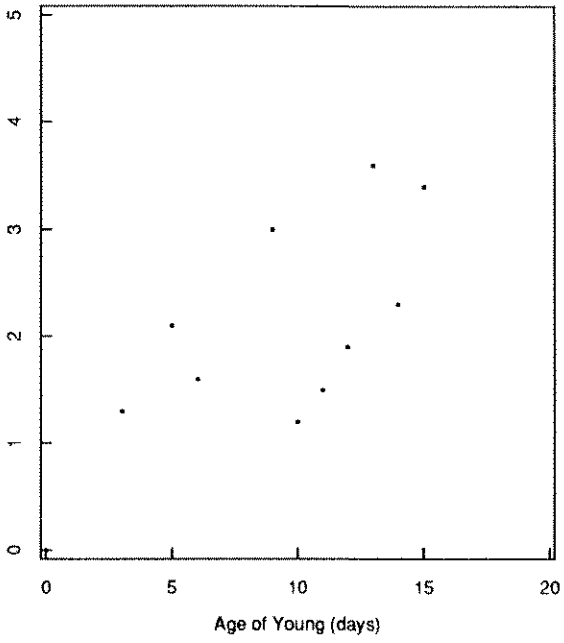
Bluebird Nest One



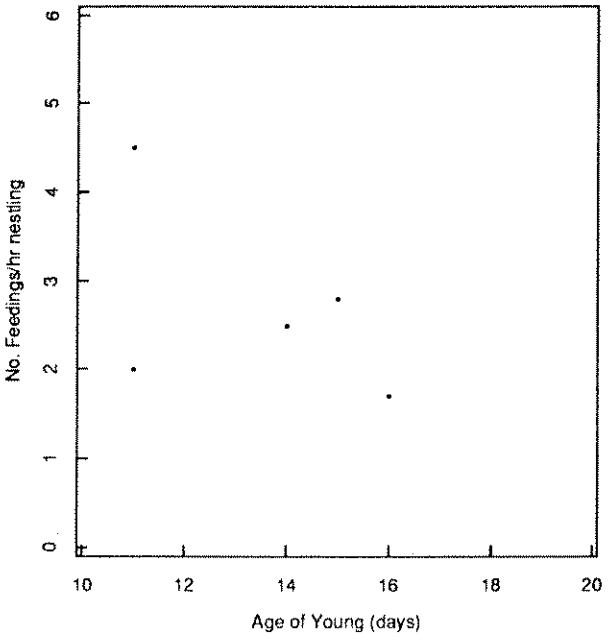
Bluebird Nest Two



Bluebird Nest Three



Bluebird Nest Four



Bluebird Nest Five

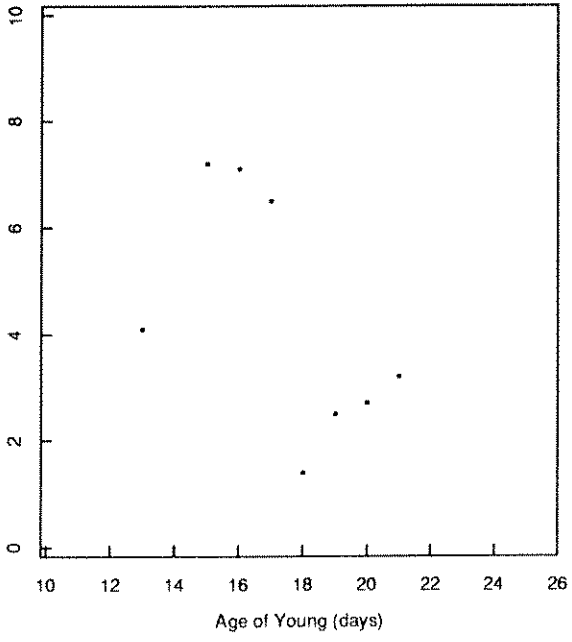


TABLE XIV. REGRESSIONS OF NESTLING AGE VERSUS ADULT FLIGHT SPEED AND VISITS TO THE NEST (FOR ALL BLUEBIRD NESTS)

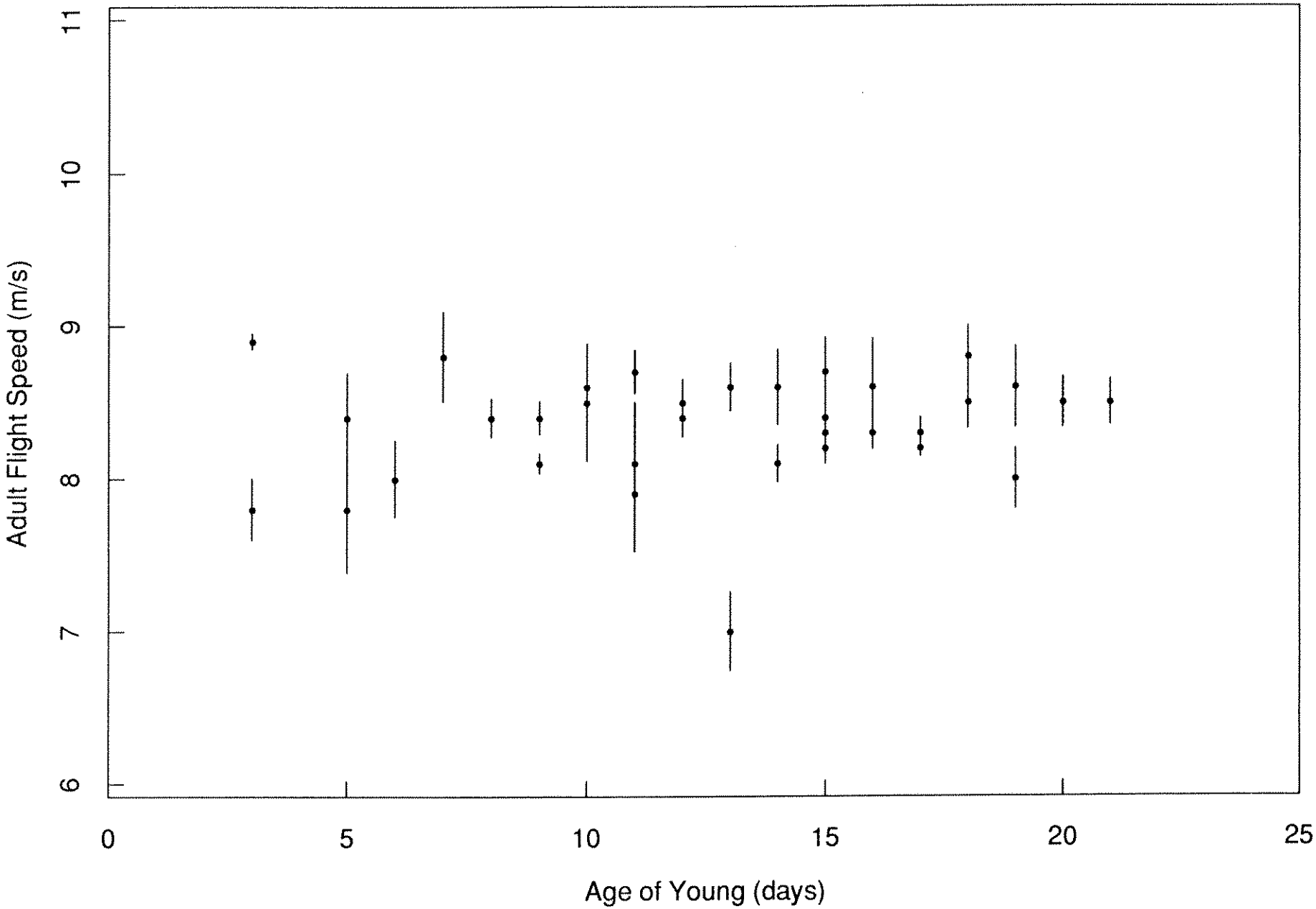
Regression	Slope (b)	Intercept	r^2	$H_o : b = 0$
Nestling age vs. Visits/hr/nestling	0.13	1.46	10.75%	$p = 0.0445$
Nestling age vs. Adult flight speed	0.012	8.20	0.41%	$p = 0.3581$

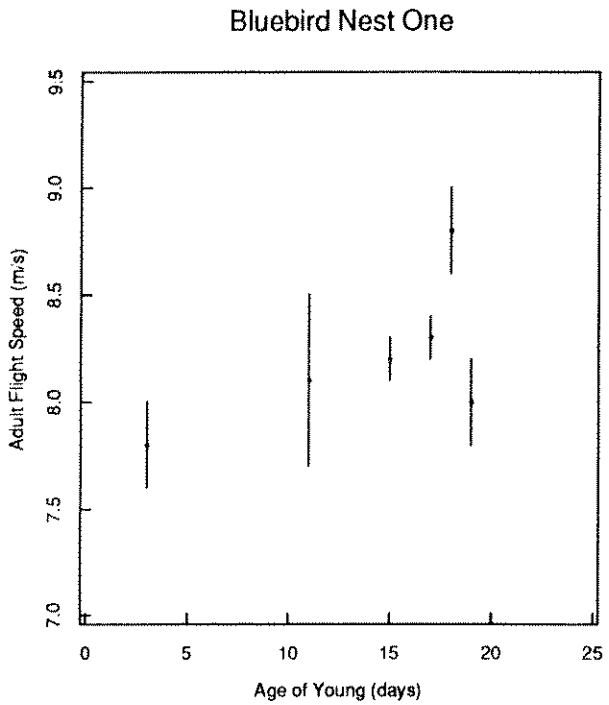
FIGURE 15. Age of Young Versus Adult Flight Speeds For All Bluebird Nests

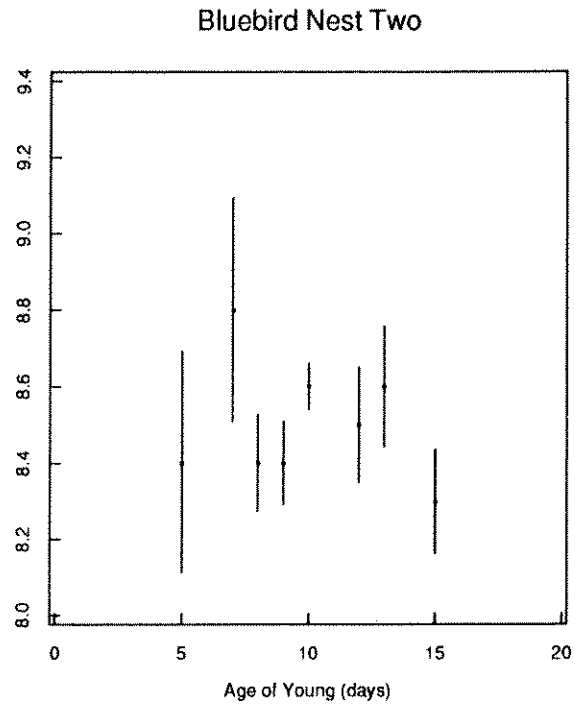
Flight speeds (ms^{-1}) from all nests are plotted against the age of the bluebird young (days). Each point represents the mean of observed speeds for a particular day from one nest, with the standard errors also shown. The results of a regression through this plot are shown in Table XIV.

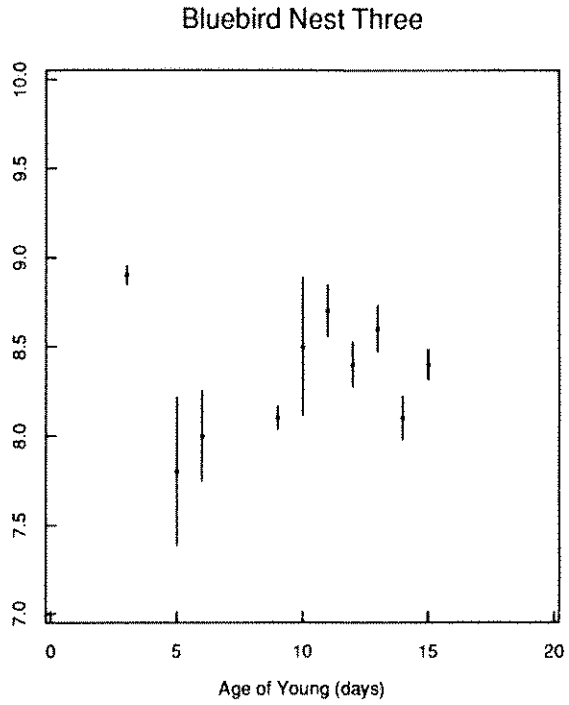
FIGURE 16. Age of Young Versus Adult Flight Speed For Individual Bluebird Nests

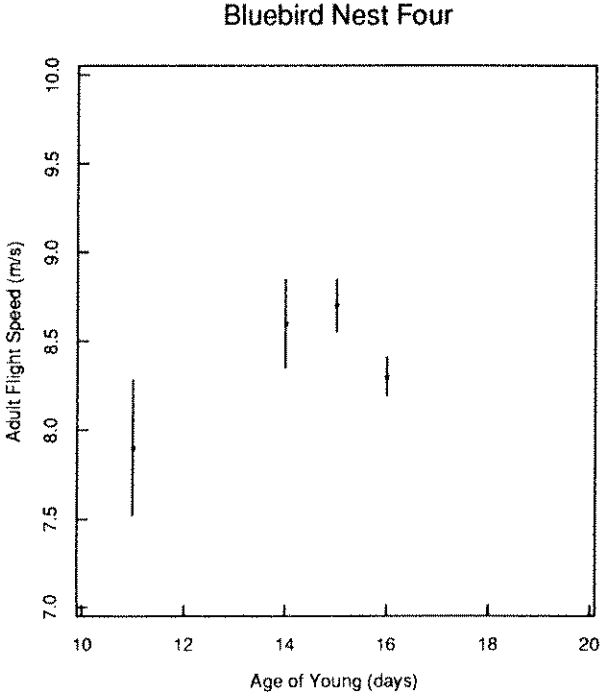
Flight speeds (ms^{-1}) from each nest are plotted against the age of the bluebird young (days). Each point represents the mean observed speed for each day, and the standard errors are also plotted.


Adult Flight Speed (m/s)
6
7
8
9
10
11
0
5
10
15
20
25
Age of Young (days)


Bluebird Nest One
Adult Flight Speed (m/s)
Age of Young (days)


Bluebird Nest Two
Age of Young (days)


Bluebird Nest Three
Age of Young (days)


Bluebird Nest Four
Adult Flight Speed (m/s)
Age of Young (days)

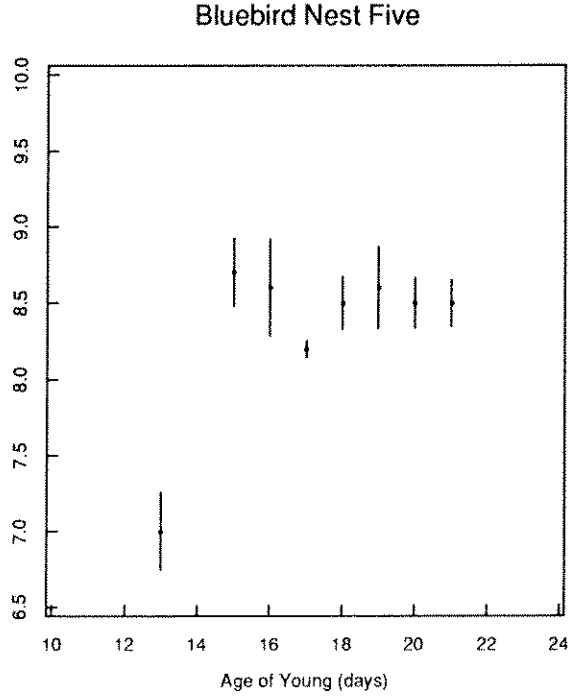

Bluebird Nest Five
Age of Young (days)

TABLE XV. ONE-WAY ANOVA TEST RESULTS FOR DIFFERENCES BETWEEN FLIGHT SPEED RECORDING DAYS

H_o : No difference in flight speeds between recording days

Nest	Recordings n	Number of Recording Days	ANOVA
Bluebird			
1	38	6	$p = 0.0174$
2	57	8	$p = 0.7886$
3	78	10	$p = 0.0011$
4	24	4	$p = 0.0946$
5	66	8	$p = 0.0013$
Tree Swallow			
1	95	7	$p = 0.1817$
2	49	5	$p = 0.0457$
3	70	6	$p = 0.0507$
4	49	5	$p = 0.0837$
5	50	5	$p = 0.9429$
Starling			
1	30	3	$p = 0.1175$
2	30	3	$p = 0.3604$
3	32	3	$p = 0.1547$
4	35	3	$p = 0.5649$
5	36	3	$p = 0.4262$

TABLE XVI. COMPARISONS OF OBSERVED SPEEDS WITH PREDICTED SPEEDS FOR INDIVIDUAL FEMALE BIRDS

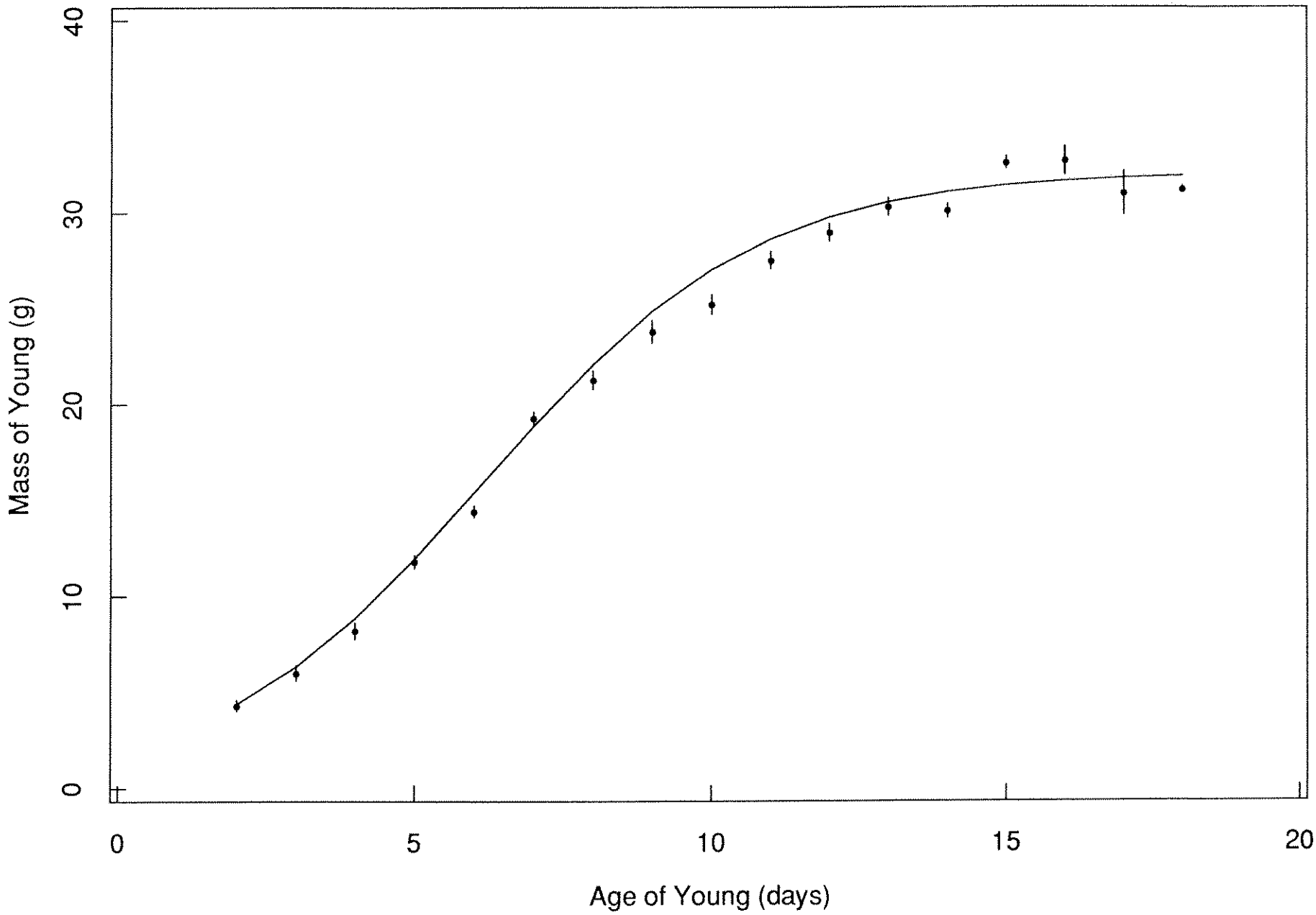
Bird	n	V_{obs} ms^{-1}	V_{mp} ms^{-1}	V_{mr} ms^{-1}	H_o : $V_{obs} = V_{mp}$	H_o : $V_{obs} = V_{mr}$
Bluebird1	17	8.1	4.6	6.7	$p < 0.001$	$p < 0.001$
Bluebird2	19	8.5	4.4	6.4	$p < 0.001$	$p < 0.001$
Bluebird3	50	8.3	4.4	6.6	$p < 0.001$	$p < 0.001$
Bluebird4	12	8.5	4.3	6.4	$p < 0.001$	$p < 0.001$
Bluebird5	42	8.3	4.5	6.6	$p < 0.001$	$p < 0.001$
Swallow2*	9	6.7	3.8	5.8	$p < 0.001$	$p < 0.001$
Swallow4*	21	6.6	3.8	5.9	$p < 0.001$	$p < 0.001$
Swallow5*	23	6.4	3.8	5.8	$p < 0.001$	$p < 0.001$

* Sex of the Tree Swallow was not determined for all flights. Only flight speeds known to be by females are noted here.

FIGURE 17. Mountain Bluebird Growth Curve

The mass of the bluebird nestlings (g) is plotted against their age (days). Each point represents the average nestling mass for a particular day. Standard errors for each point are also plotted. The fitted line represents a logistic growth curve, and the equation of the line is

$$Y = \frac{32.075}{1 + 14.24e^{-.446X}}$$


Mass of Young (g)
0
10
20
30
40
0
5
10
15
20
Age of Young (days)

3.4 DISCUSSION

To determine the optimal speed, V_{opt}, at which to bring food to the nest, as predicted by Norberg (1981), the net rate of energy gain during foraging, P_{gain}, must first be known. The model assumes that the adult bird balances its own energy budget and the net rate of energy gain thus does not include the adults' cost of foraging or maintenance. If the foraging rate and value of prey items are known, P_{gain} can easily be calculated. An alternative method to determine P_{gain} is to view the net energy gained during foraging as that taken to the nest (the gross energy required for the nestlings) plus the amount of energy for travelling flight. This can be viewed by rearranging equation 16, to give

$$P_{gain} = \frac{\Delta E_1 + P_{air} t_{air}}{t_{for}} \tag{24}$$

where ΔE_1 can be considered the amount of energy brought to the nest.

If the observed flight speeds of the birds studied corresponded to the V_{opt} as predicted by Norberg (*i.e.* they were flying at the optimal speed to deliver a given amount of energy to the young), then P_{gain} could be determined by simply finding a new tangent to the curve at V_{obs} for each species. This is done by setting V_{obs} as the smallest ratio of P/V, instead of V_{mr}. The vertical dotted line in Figure 18 shows the position of V_{obs} for the Mountain Bluebird while the slanted dotted line represents the tangent to this point. The Y-intercept of this line indicates the value of P_{gain}, if V_{obs} is considered to be V_{opt}. Using this method, P_{gain} for the Mountain Bluebird is shown to be $0.48W$ (Figure 18) and $0.12W$ for the Tree Swallow (Figure 19).

To decide if the above values of P_{gain} were sufficient to support the nestlings plus the costs of flight, nestling energy requirements were first determined, as outlined below.

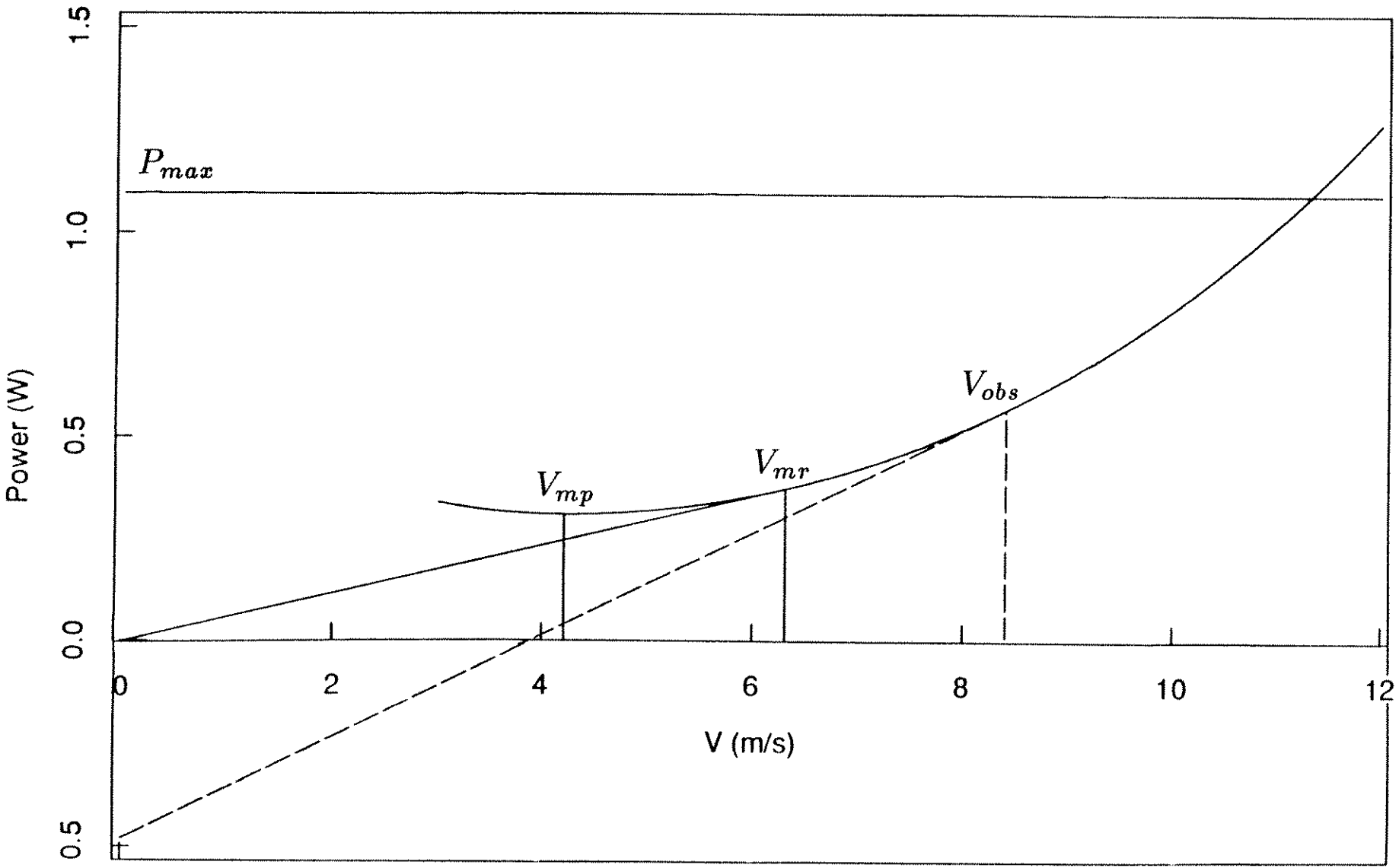
Only a percentage of the gross energy intake (the energy that is consumed by the young birds) is eventually used for the maintenance and growth of the nestling. The rest is lost as wastes or expended during assimilation. Outlines of the distribution of the gross

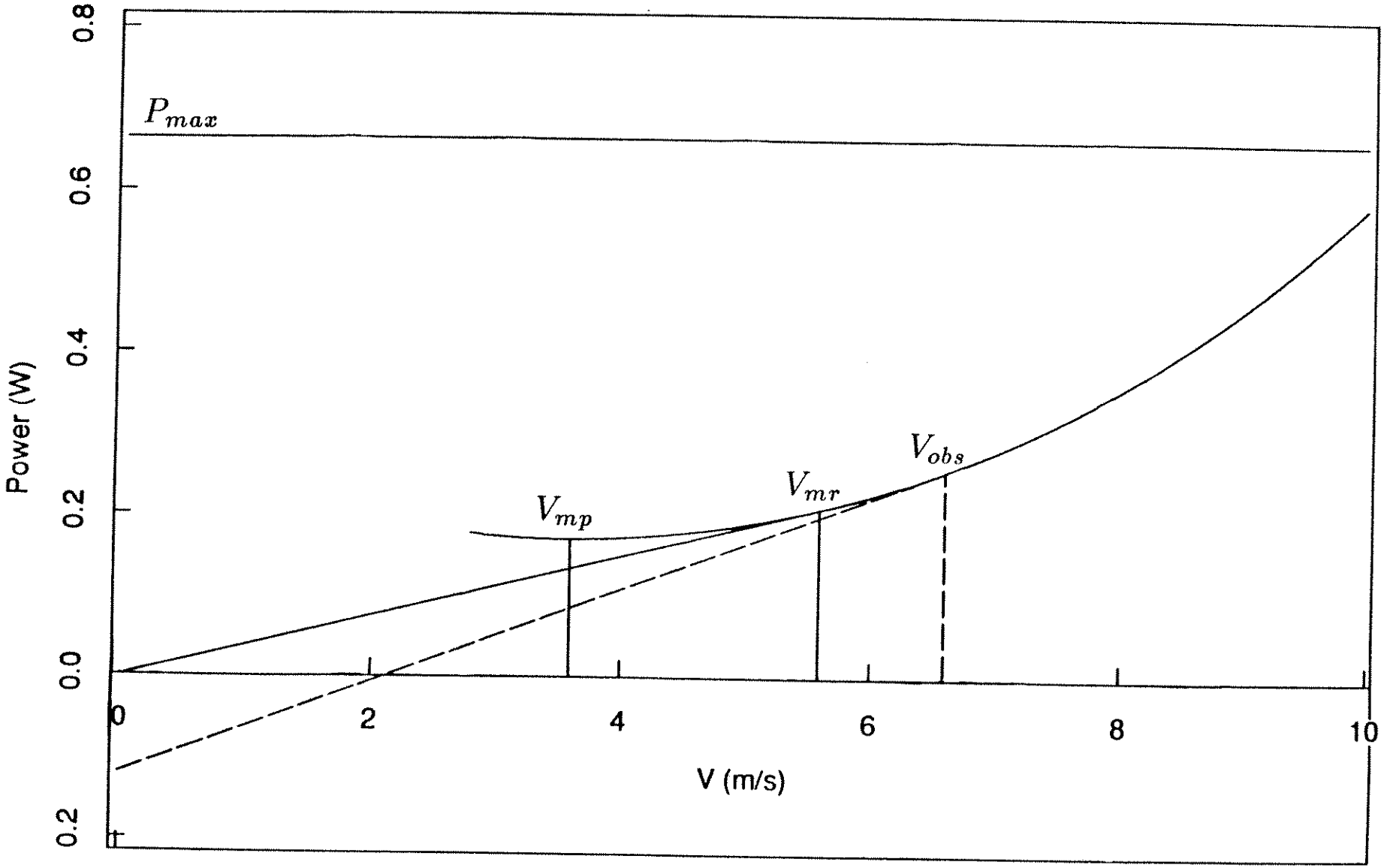
FIGURE 18. Determination of P_{gain} for the Mountain Bluebird

Power for flight (W) versus flight velocity (ms^{-1}) is plotted, for the Mountain Bluebird. V_{mp}, V_{mr}, and V_{obs} are defined, as is P_{max}. The sloped dotted line represents the tangent to V_{obs}, and thus the Y-intercept indicates P_{gain} if V_{obs} is taken to be V_{opt}.

FIGURE 19. Determination of P_{gain} for the Tree Swallow

Power for flight (W) versus flight velocity (ms^{-1}) is plotted, for the Tree Swallow. V_{mp}, V_{mr}, and V_{obs} are plotted, as is P_{max}. The sloped dotted line represents the tangent to V_{obs}, and thus the Y-intercept indicates P_{gain} if V_{obs} is taken to be V_{opt}.


1.5
1.0
0.5
0.0
0.5
Power (W)
P_{max}
V_{obs}
V_{mr}
V_{mp}
0
2
4
6
8
10
12
V (m/s)


0.8
0.6
0.4
0.2
0.0
0.2
Power (W)
P_{max}
V_{mp}
V_{mr}
V_{obs}
0
2
4
6
8
10
V (m/s)

energy can be found in Ricklefs (1974), King and Farner(1961) and O'Connor (1984). Following O'Connor (1984), the portion of the Gross Energy Intake (GEI) that is actually metabolized by the bird each day is termed the Daily Energy Budget (DEB). The DEB is the sum of Existence Metabolism (EM) and Productive Energy (PE). EM is the rate of energy used to maintain a constant mass, while PE is the energy available for activities such as growth.

Ricklefs (1974) states that biosynthetic work (growth or PE) can be estimated if growth rate, energy density and the net efficiency of synthesis for the nestling are all known. Since masses for the second brood of Mountain Bluebird nestlings were recorded each day, starting at the age of two days, the growth rate in terms of increased mass per day is known. A logistic growth curve fitted to the nestling mass measurements is shown in Figure 28. The form of the growth curve is

$$Y = \frac{\alpha}{1 + \beta e^{\gamma X}} \tag{25}$$

where α, β, and γ are coefficients, and Y and X are coordinates of a point on the curve.

Energy density can be expressed as

$$D = 4.1868(a + bW) \tag{26}$$

where D is the energy density (kJg^{-1}), W is the percent of adult body mass, and a and b are coefficients (Ricklefs, 1974). Since energy density has been determined for only a few species, the average values of a and b for seven passerine species (Ricklefs, 1974 Table 24) were used to describe the nestling Mountain Bluebird relationship. This procedure was also followed by Walsberg (1978). Energy densities were thus estimated for each nestling mass. Net efficiency of synthesis was estimated as 75% (Ricklefs, 1974). The energy required for growth, then can be expressed as

$$PE = \frac{D \times \text{growth rate}}{0.75} \tag{27}$$

where PE is expressed in kJd^{-1}.

Existence metabolism can be approximated as the adult's mass-specific metabolic rate (Walsberg, 1978, Ricklefs, 1974). Table XVII lists the estimates of EM, PE, DEB, and GEI for the bluebird nestlings at each mass.

The efficiency of assimilation determines the additional energy (resulting in the GEI) required to maintain the daily energy budget (O'Connor, 1984). Assimilation efficiencies range from $60 - 80\%$ (Table 6.1, O'Connor, 1984). Ricklefs (1974) notes that assimilation efficiencies for insect diets ranges from $70 - 80\%$. A value of 70% assimilation efficiency is used in this study.

The gross energy intake, then, is approximated by summing the energy requirements for nestling growth and maintenance and dividing by the assimilation efficiency. This gross energy intake must also take into account the number of nestlings and the amount of time available spent foraging by the adults (Table XIII).

$$\text{Gross energy required per nestling} = \frac{PE(kJd^{-1}) + EM(kJd^{-1})}{0.70} \tag{28}$$

The energy requirement will be expressed as kJd^{-1}, but the unit of day must be the amount of the day available for foraging, not the 24-hour day, because the parents will have to supply the required energy in a limited time. For the Mountain Bluebird, the time available for foraging is approximately 16 hours per day at the study site (personal observation).

Some error in the energy calculations may be due to the fact that the nestling masses and thus the growth rate were determined for the second brood of nestlings while flight speed measurements were recorded while the adults were raising the first brood. Growth rates are known in some cases to be slightly different between first and second broods

(Ricklefs, 1968). However, the second broods all contained four nestlings each, which was the case for four of five of the first broods, so energy demands on the parents were thought to be similar. A growth curve was plotted using Mountain Bluebird nestling masses of first and second broods obtained by Power (1966) and the coefficients of the logistic growth curve equation were similar when compared to the coefficients determined from this study (coefficients of α, β, and γ from Power's data were 24.87, 13.44, and -0.44, while from the present study they were 32.06, 14.24, and -0.45 respectively). The coefficient β is a constant proportional to the overall growth rate and may be used as a comparison between and within species.

The minimum energy required during the nestling period by the nestlings will be at the age of one day. Since measurements of mass were not started until the young were two days old, the first growth rate cannot be obtained until day three, when the increase in mass from day two to day three can be determined. Thus, day three is considered here as the minimum known energy requirement to be brought to the nest. Values of the gross energy intake (GEI) for one nestling at each mass are listed in Table XVII. Since four of the five nests studied consisted of four young, and assuming that each parent fed the young equally, GEI is considered for one adult bluebird to be the rate of energy delivered for two nestlings. The minimum GEI required when two young are three days old is 0.89 Watts. The maximum GEI occurs when two young are fifteen days old (GEI= $3.8W$). An average GEI over the nestling period is $2.33W$.

Walsberg (1983) has determined a general expression for average and peak energy expenditure of nestlings based on a regression of data from ten species. Average energy expenditure per nestling is written as

$$ln(E_{\bar{N}}) = ln14.05 + 0.440lnM \tag{29}$$

where M is the adult body mass (in g) and $E_{\bar{N}}$ is the average energy expenditure per nestling (kJd^{-1}). Peak energy expenditure is

$$ln(E_N) = ln13.40 + 0.528lnM \quad (30)$$

where E_N is the peak energy expenditure per nestling (kJd^{-1}). $E_{\bar{N}}$ and E_N are energy for growth and maintenance of the young only and must also be corrected to gross energy intake. Table XIX shows similar results of the Walsberg (1983) equations and for peak and average energy expenditures per nestling determined by following O'Connor (1984) and Ricklefs (1974), for the Mountain Bluebird and Tree Swallow.

Nestling energy requirements for the Tree Swallow (Table XVIII) were calculated in the same manner as for the Mountain Bluebird nestlings. Nestling masses from Paynter (1954) were used since swallow nestlings in this study were not weighed. The estimate of gross energy requirements brought by the parents was based on 2.5 nestlings for each parent since three of the five nests consisted of five young. The other two nests were each of six young so would be underestimated. The minimum nestling energy requirement for one nestling was determined to be $0.19W$. These nestling energy estimates may not be very accurate because nestling masses were used of nestlings from a different study and study location, and also because the calculations themselves are only a rough approximation of nestling energy requirements. Comparisons of the peak and average nestling energy expenditures with those calculated using Walsberg's equations, however, indicate similar results (Table XIX).

Upon comparing the values of P_{gain} determined when V_{obs} is assigned as V_{opt} with the estimated nestling energy requirements, it appears that V_{obs} is not a good approximation to V_{opt}. For the Mountain Bluebird, P_{gain} determined from Figure 18 was found to be $0.48W$, while the minimum nestling requirement for two nestlings at the age of three days was estimated as $0.89W$. P_{gain}, then, clearly does not cover the cost of feeding two young, even at three days old. It would also not cover the cost of the travelling flight, as indicated in equation 16. The difference between energy required by the nestlings and energy apparently delivered may be partially explained by the observation that the

TABLE XVII. MOUNTAIN BLUEBIRD NESTLING ENERGY REQUIREMENTS

Age (days)	**Percent of Adult Mass** (%)	**EM** (kJd^{-1})	**PE** (kJd^{-1})	**DEB** (kJd^{-1})	**GEI** (W) (1 nestling)
3	21.1	8.65	9.23	17.87	0.443
4	28.8	11.82	13.05	24.87	0.6118
5	41.4	17.01	24.38	41.39	1.027
6	50.5	20.76	19.17	39.93	0.9903
7	67.7	27.82	41.75	69.57	1.725
8	74.7	30.71	17.97	48.68	1.207
9	83.5	34.31	23.90	58.21	1.444
10	88.4	36.33	14.74	51.07	0.802
11	96.5	39.64	23.98	63.62	1.578
12	102.0	41.75	16.20	57.95	1.437
13	106.0	43.68	14.39	58.07	1.440
14	106.0	43.39	-2.2	41.19	1.022
15	114.0	47.00	28.97	75.97	1.884
16	115.0	47.13	1.17	48.31	1.198
17	109.0	44.69	-19.15	25.54	0.6334
18	109.0	44.98	2.25	47.23	1.171

TABLE XVIII. TREE SWALLOW NESTLING ENERGY REQUIREMENTS

Age (days)	**Percent of Adult Mass** (%)	**EM** (kJd^{-1})	**PE** (kJd^{-1})	**DEB** (kJd^{-1})	**GEI** (W) (1 nestling)
2	11.3	3.58	4.05	7.63	0.189
3	17.6	5.58	6.53	12.11	0.300
4	26.0	8.27	9.71	17.98	0.4459
5	38.5	12.24	16.44	28.68	0.711
6	45.6	14.50	10.01	24.51	0.6078
7	64.6	20.54	31.58	52.12	1.293
8	82.1	26.10	33.16	59.26	1.470
9	93.6	29.76	14.64	44.40	1.101
10	100.7	32.02	10.82	42.83	1.062
11	105.8	33.64	-2.10	31.54	0.782
12	104.9	33.36	-1.00	32.36	0.803
13	104.4	33.19	3.18	36.37	0.902
14	105.9	33.67	1.11	34.77	0.862
15	106.4	33.83	-3.10	30.72	0.762
16	105.0	33.38	-1.65	31.73	0.787
17	104.2	33.13	-8.42	24.70	0.6127
18	100.4	31.92	-2.67	29.25	0.725
19	99.1	31.51	-4.02	27.48	0.682
20	97.2	30.90	-6.70	24.20	0.600

TABLE XIX. COMPARISONS OF NESTLING ENERGY EXPENDITURES FOR ONE NESTLING

	Peak Nestling Expenditure kJd^{-1}	Average Nestling Expenditure kJd^{-1}
Mountain Bluebird		
Estimated	108.5	67.0
Walsberg (1983)	112.2	87.6
Tree Swallow		
Estimated	84.7	44.6
Walsberg (1983)	85.4	48.9

adults sometimes caught prey items within a few metres of the nest, thus increasing energy delivery to the young.

Similar conclusions can be reached when comparing P_{gain} with the Tree Swallow nestling energy requirements. The value of P_{gain} when V_{obs} is considered to be V_{opt} is $0.12W$, while the minimum requirement for 2.5 nestlings is $0.47W$, at the age of two days. Again, this does not take into account the flight costs.

The results indicate that adult flight speeds do not vary with increasing age and size of the young for the Mountain Bluebird and the Tree Swallow. A fairly constant velocity is used throughout the nestling period for the Mountain Bluebird. The number of visits to each nestling per hour does increase slightly and significantly with the age of the nestlings, but the r^2 value is only 11%, meaning that only 11% of the variation in feedings can be explained by the variation in nestling age. As seen in Figures 14, there was no general trend common to all nests with increasing nestling age. Since neither visiting frequency nor flight velocity of the bluebird parents increased with nestling age, in order to bring sufficient energy supplies to the young the parents must either spend more hours of the day foraging or make up for this discrepancy in periods of the day that were not under observation. Since each nest was usually observed for only one hour per day, the whole daily activity schedule was not fully known. One bluebird nest, however, was observed for a whole day but cannot be used in comparisons with nestling ages. It is possible that the parents increase their feeding rates during other periods of the day. This is supported by the fact that the feeding rate was quite variable, ranging from $0.7 - 7.2$ feedings per hour per nestling.

That feeding rates were increased during other parts of the day is also probably true for the Tree Swallow, which also had a variable feeding rate ($1.3 - 9.4$ visits/hr nestling). Flight speeds of the Tree Swallow were taken starting when the young were one or two days old and continued only until they were six or seven days old. Since only the first week of the nestling period was observed, it is possible that the flight speed of the adults may have increased when the young became older, with greater energy demands. The observed

speed ($V_{obs} = 6.6ms^{-1}$) seemed to be fairly constant over the first week. Table XV shows that only at nest two was there any difference in flight speeds between any of the recording days.

It seems clear that the flight velocity remained constant at close to $8.4ms^{-1}$ for the Mountain Bluebird and $6.6ms^{-1}$ for the Tree Swallow. There were differences within different nests between recording days for nests one, three and five but these were all due to only one recording day being different from the rest (Table XV). Female bluebirds and swallows definitely flew at speeds greater than the maximum range speed predicted from their own individual power curves (Table XVI) and the mean velocity of all birds probably did not correspond to V_{opt} as predicted by Norberg (1981).

CHAPTER FOUR

GENERAL DISCUSSION AND CONCLUSIONS

4.1 GENERAL DISCUSSION

Morphological designs, especially wing dimensions, are important in determining and limiting bird flight speeds. More specialized birds are adapted to using their particular environment, and their body design in relation to flight behaviours and performance is also specialized (Rayner, 1985*b*). This leads to a rigidity of design "optimality" for a particular habitat and lifestyle.

The effect of wing dimensions on flight can be characterized by the wing loading (weight per unit wing area) and the aspect ratio (wing span squared over the wing area). Birds that have a high wing loading tend to be fast fliers, and also have a high stalling speed, V_{stall}, to avoid. High aspect ratio wings can also contribute to high speed flight (for example ducks, geese, grebes, and some shorebirds), although, when combined with low wing loadings as in swifts, swallows, and terns, for example, minimum power and maximum range speeds are reduced because of diminished induced power requirements for flight. Such birds can afford to fly at slower velocities, although a disadvantage to this is that their speed at which the cost of transport is minimimized is relatively low.

The Tree Swallow, White-throated Swift, and Black Tern, all aerial insectivores, were found in this study to fly faster than V_{mr}. The Black Tern has a high aspect ratio (10.4) and a low wing loading ($19.1 Nm^{-2}$), which suggests that its power requirements, and thus V_{mr}, would have been relatively lower than for the other species. However, the Tree Swallow, which has an approximately average aspect ratio (7.4) and low wing loading ($13.9 Nm^{-2}$) also flew faster than V_{mr}, as did the swift (with $AR = 11.9$ and $Q = 34.7 Nm^{-2}$). Figure 2 shows that although the aspect ratios of these three species differ, the general shape of the wing is similar.

The starling and the bluebird were found to have similar aspect ratios (6.7 and 5.9 respectively) with similar wing shapes (Figure 2) but the starling had a higher wing loading ($Q = 36.6Nm^{-2}$ compared to $Q = 17.2Nm^{-2}$ for the bluebird). The difference in Q is due almost completely to the difference in mass between the two species, since the wing areas are quite similar (Table II). Both species fly faster than V_{mr}, although their foraging styles are quite different - the starling forages mainly from ground level, while the bluebird often detects prey by hovering above the ground and thus may potentially spend more energy in flight during foraging.

It is clear, therefore, that the above five species flew speeds greater than the maximum range speed, V_{mr} when the adult birds were flying to and from a foraging site while rearing their young. The relation of V_{obs} to V_{mr} appeared to be independent of aspect ratios and wing loadings as well as the habitat (open rangelands, marshes, mountainous terrain) and foraging style (ground foragers, aerial foragers, and even the case of the Black Tern which sometimes catches fish).

The Pigeon Guillemot and Red-necked Grebe both fly at speeds significantly less than V_{mr}, and in the case of the grebe, less than V_{mp} as well. Both species have similar aspect ratios (8.8 for the grebe and 7.5 for the guillemot - Figure 1) and high wing loadings compared to the preceding five species (Table II). This would suggest that they should be fast fliers, at least flying at V_{mr}, but this was not confirmed in the results.

A possible explanation of the speeds observed for the Pigeon Guillemot is that the birds were not actually feeding young. They were observed leaving and returning to particular crevices in the rock cliffs, but no nestlings were observed, and since it was early in their breeding season, it is possible that the speeds recorded represented foraging flights of adults with no extra demands from young. Even if this were so, V_{mr} would still be the predicted flight speed for foraging flights in order to minimize the trip costs per unit distance travelled. Another possibility is that since this species also uses its wings for under water propulsion, the wings may be also adapted for under water use, and not exclusively for flight.

The Red-necked Grebe, however, was observed carrying fish to its young and its mean recorded flight speed was significantly less than even the minimum power speed, V_{mp}. The range of its speeds shown by the boxplot in Figure 10 indicate that some of the speeds were less than the theoretical V_{stall}. Clearly other factors besides bringing the maximum amount of food to the young determine the flight speed for the Red-necked Grebe.

In a more detailed study of breeding Mountain Bluebirds and Tree Swallows, an estimate of P_{gain}, the net rate of energy gained during foraging, was determined using Norberg's (1981) model. P_{gain} was determined by setting V_{obs} as the optimal speed, V_{opt}, and drawing a tangent to this point (Figures 18, 19). This value of P_{gain} was then compared to nestling energy requirements for both species and P_{gain} in both cases was found to be less than the minimum nestling energy requirements. Since P_{gain} should also include the cost of the travelling flight (equation 16), it appears that both the P_{gain} estimated and thus the observed flight speed, V_{obs}, were much less than those predicted by Norberg (1981). It appears, then, that Mountain Bluebirds and Tree Swallows in this study flew at speeds intermediate between V_{mr} and V_{opt}.

Since flight speed of foraging trips did not increase with the age of the young and the feeding rate to each nestling per hour was also independent of nestling age, it is possible that, in order to meet the increasing energy demands of their young, the adults increased their foraging rate (although probably not their flight speed as it appeared to be constant independent of the time of day of the recording - Figures 11, 12) and delivery rate to the young at some other period during the day not under observation.

4.2 CONCLUSIONS

1. Five species (Tree Swallow, Mountain Bluebird, European Starling, White-throated Swift, and Black Tern) were found to fly at speeds greater than their maximum range speed, V_{mr}, when flying to and from a foraging site while raising their young.

2. The relation of the observed flight velocity, V_{obs}, to V_{mr} for the above five species appeared to be independent of morphology, foraging style, and habitat.

3. The two species (Pigeon Guillemot and Red-necked Grebe) which flew slower than V_{mr} were both larger birds with much higher wing loadings. Flight speed in the Pigeon Guillemot may not have been related to rearing its young since they may not have been hatched at the time of the recordings.

4. Flight speeds of adult Mountain Bluebirds remained fairly constant over the nestling period at $8.4ms^{-1}$, and did not increase with increasing age of the young. For the Mountain Bluebird, the number of visits to the nest per hour per nestling did not increase with the age of the nestling. Flight speeds of adult Tree Swallows also remained constant over the recording period, with $V_{obs} = 6.6ms^{-1}$.

5. When V_{obs} was assigned as V_{opt} for the Mountain Bluebird and Tree Swallow the corresponding value of P_{gain} was less than the minimum nestling energy requirement. This indicates that the two species studied did not fly at the predicted V_{opt}, but at an intermediate speed between V_{mr} and V_{opt}.

6. In order to meet nestling energy requirements, Mountain Bluebirds and Tree Swallows probably increase their feeding rate at times of the day other than those that were under observation. This idea is supported by the variable feeding rate of both species ($0.7-7.2$ visits per hour per nestling for the Mountain Bluebird and $1.3-9.4$ visits per hour per nestling for the Tree Swallow). Flight speeds were probably not increased for the Mountain Bluebird as they appeared to be constant independent of the time of day of the recording. Flight speed for the Tree Swallow may have increased later in the season as only the first week of the nestling period was studied.

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APPENDIX

Tables A1 - A10

Observations at Mountain Bluebird and Tree Swallow Nests

TABLE A1. OBSERVATIONS FOR BLUEBIRD NEST ONE

Date	Nestling Age (days)	Observation Duration (min)	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed (ms^{-1}), n
			male	female	total		
May 25	3						7.8, 6
June 1	10	50	9	7	16	3.2	
June 2	11	30	2	0	2	0.7	8.1, 6
June 2	11	26	4	1	5	1.9	8.1, 6
June 5	15	60	2	5	7	7.0	8.2, 5
June 7	17	59	3	2	5	5.1	8.3, 7
June 8	18	57	1	5	6	6.3	8.8, 9
June 9	19	55	2	1	3	3.3	8.0, 5
TOTAL		337	23	21	44		

* Number visits/hr/nestling

TABLE A2. OBSERVATIONS FOR BLUEBIRD NEST TWO

Date	Nestling Age (days)	Observation Duration (min)	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed (ms^{-1}), n
			male	female	total		
June 4	5	55	5	6	11	3.0	8.4, 5
June 6	7	59	14	7	21	5.3	8.8, 13
June 7	8	35	2	2	4	1.7	8.4, 4
June 8	9	26	3	1	4	2.3	8.4, 5
June 9	10	27	1	2	3	1.7	8.6, 2
June 11	12	42	7	6	13	4.6	8.5, 12
June 12	13	61	8	7	15	3.7	8.6, 10
June 14	15	30	1	1	2	1.0	8.3, 6
TOTAL		335	41	32	73		

* Number visits/hr/nestling

TABLE A3. OBSERVATIONS FOR BLUEBIRD NEST THREE

Date	Nestling Age (days)	Observation Duration (min)	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed (ms^{-1}), n
			male	female	total		
June 5	3	60	3	2	5	1.3	8.9, 2
June 7	5	58	5	3	8	2.1	7.8, 5
June 8	6	58	2	4	6	1.6	8.0, 6
June 11	9	61	6	6	12	3.0	8.1, 13
June 12	10	37	1	2	3	1.2	8.5, 3
June 13	11	62	0	6	6	1.5	8.7, 7
June 14	12	40	3	2	5	1.9	8.4, 9
June 15	13	25	1	5	6	3.6	8.6, 10
June 16	14	45	2	5	7	2.3	8.1, 9
June 17	15	40	3	6	9	3.4	8.4, 14
TOTAL		486	26	41	67		

* Number visits/hr/nestling

TABLE A4. OBSERVATIONS FOR BLUEBIRD NEST FOUR

Date	Nestling Age (days)	Observation Duration (min)	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed (ms^{-1}), n
			male	female	total		
June 2	11	20	1	5	6	4.5	7.9, 3
June 2	11	15	2	0	2	2.0	
June 5	14	61	1	9	10	2.5	8.6, 4
June 6	15	58	4	7	11	2.8	8.7, 11
June 7	16	43	3	2	5	1.7	8.3, 6
TOTAL		197	11	23	34		

* Number visits/hr/nestling

TABLE A5. OBSERVATIONS FOR BLUEBIRD NEST FIVE

Date	Nestling Age (days)	Observation Duration (min)	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed $(ms^{-1}), n$
			male	female	total		
June 4	13	59	8	8	16	4.1	7.0, 8
June 6	15	58	8	20	28	7.2	8.7, 16
June 7	16	57	6	21	27	7.1	8.6, 13
June 8	17	62	4	4	8	6.5	8.2, 6
June 9	18	43	2	2	4	1.4	8.5, 9
June 10	19	18	2	1	3	2.5	8.6, 3
June 11	20	39	3	4	7	2.7	8.5, 9
June 12	21	38	1	1	2	3.2	8.5, 2
TOTAL		374	34	61	95		

* Number visits/hr/nestling

TABLE A6. OBSERVATIONS FOR SWALLOW NEST ONE

Date	Observation Duration	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed
	(min)	male	female	total		$(ms^{-1}), n$
June 12	22	2	1	3	1.4	6.9, 1
June 14	22			15	6.8	6.8, 19
June 15	26	5	9	14	5.4	6.5, 24
June 16	30	2	8	10	3.3	6.5, 18
June 17	17	6	10	16	9.4	6.9, 10
June 18	30					6.8, 10
TOTAL	157			58		

* Number visits/hr/nestling

TABLE A7. OBSERVATIONS FOR SWALLOW NEST TWO

Date	Observation Duration (min)	Number of Visits to Nest male	female	total	Feeding Rate *	Mean Flight Speed (ms^{-1}), n
June 14	28			5	2.1	6.2, 7
June 15	44			5	1.4	6.5, 9
June 16	45	3	2	5	1.3	7.0, 10
June 17	40			8	2.4	6.7, 13
June 18	30					6.6, 10
TOTAL	157			23		

* Number visits/hr/nestling

TABLE A8. OBSERVATIONS FOR SWALLOW NEST THREE

Date	Observation Duration (min)	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed (ms^{-1}), n
		male	female	total		
June 13	58	3	5	8	1.4	6.4, 8
June 14	47	3	3	6	1.3	6.2, 11
June 15	52	4	7	11	2.1	6.6, 15
June 16	51	4	4	8	1.6	6.9, 12
June 17	29	4	4	8	2.8	6.6, 14
June 18	30					6.7, 10
TOTAL	267			41		

* Number visits/hr/nestling

TABLE A9. OBSERVATIONS FOR SWALLOW NEST FOUR

Date	Observation Duration (min)	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed (ms^{-1}), n
		male	female	total		
June 14	30			5	2.0	6.8, 8
June 15	30	3	3	6	2.4	6.3, 11
June 16	21	2	3	5	2.9	6.4, 10
June 17	29			5	2.1	6.6, 10
June 18	30					6.7, 10
TOTAL	140			21		

* Number visits/hr/nestling

TABLE A10. OBSERVATIONS FOR SWALLOW NEST FIVE

Date	Observation Duration (min)	Number of Visits to Nest			Feeding Rate *	Mean Flight Speed (ms^{-1}), n
		male	female	total		
June 14	22			5	2.7	6.3, 9
June 15	35	3	3	6	2.1	6.4, 10
June 16	29	1	4	5	2.1	6.3, 11
June 17	30	2	4	6	2.4	6.5, 10
June 18	30					6.5, 10
TOTAL	146			22		

* Number visits/hr/nestling