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**Abstract**—The recent development of the pop-up satellite archival tag (PSAT) has allowed the collection of information on a tagged animal, such as geolocation, pressure (depth), and ambient water temperature. The success of early studies, where PSATs were used on pelagic fishes, has spurred increasing interest in the use of these tags on a large variety of species and age groups. However, some species and age groups may not be suitable candidates for carrying a PSAT because of the relatively large size of the tag and the consequent energy cost to the study animal. We examined potential energetic costs to carrying a tag for the cownose ray (*Rhinoptera bonasus*). Two forces act on an animal tagged with a PSAT: lift from the PSAT's buoyancy and drag as the tag is moved through the water column. In a freshwater flume, a spring scale measured the total force exerted by a PSAT at flume velocities from 0.00 to 0.60 m/s. By measuring the angle of deflection of the PSAT at each velocity, we separated total force into its constituent forces—lift and drag. The power required to carry a PSAT horizontally through the water was then calculated from the drag force and velocity. Using published metabolic rates, we calculated the power for a ray of a given size to swim at a specified velocity (i.e., its swimming power). For each velocity, the power required to carry a PSAT was compared to the swimming power expressed as a percentage, %TAX (Tag Altered eXertion). A %TAX greater than 5% was felt to be energetically significant. Our analysis indicated that a ray larger than 14.8 kg can carry a PSAT without exceeding this criterion. This method of estimating swimming power can be applied to other species and would allow a researcher to decide the suitability of a given study animal for tagging with a PSAT.

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## Quantification of drag and lift imposed by pop-up satellite archival tags and estimation of the metabolic cost to cownose rays (*Rhinoptera bonasus*)\*

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The pop-up satellite archival tag (PSAT) was developed in the late 1990s primarily for the tracking of large pelagic fish (Arnold and Dewar, 2001; Gunn and Block, 2001). This electronic tag is attached to a large fish, collects data on the environment of the fish for a preprogrammed period, and then detaches from the fish by corrosion of a release pin. A float on the tag carries the tag to the surface of the water where the PSAT begins transmitting the archived environmental data. The pop-up location is determined by the Argos satellites that in turn transmit the data to a relay station. The earliest uses of these tags have been on large pelagic fishes such as Atlantic bluefin tuna (*Thunnus thynnus*) (Block et al., 1998; Lutcavage et al., 1999) and blue marlin (*Makaira nigricans*) (Graves et al., 2002). In the early tuna studies, PSATs were used to investigate geographic range and possible stock structure. Graves et al. (2002) used the tags to assess postrelease survival of blue marlin from the recreational fishery. Over their short history, the PSATs have been improved to collect even more data than the original models and currently record light levels, temperature, and pressure readings. The light levels are used to estimate geolocation and the pressure readings are converted to depth measurements. Combined with the temperature readings, the depth measurements can provide detailed information about the study animal's swimming behavior. Experiences with the first-generation tags led to the

development of various fail-safe features (Arnold and Dewar, 2001). Both premature detachment (made evident by the tag floating at the surface) or lack of vertical movement (i.e., constant depth, which indicates probable death of the animal) initiate early transmission of archived data. Should the tag be carried to an extreme depth where water pressure might physically crush the tag, release mechanisms, both software-based and mechanical, have been developed to free the tag from the animal.

PSATs were developed to supplement the tracking data that could be acquired through acoustic tagging and archival tagging. Acoustic tagging is most useful for studying fine-scale movement and habitat use and for collecting physiological data (Arnold and Dewar, 2001; Gunn and Block, 2001). However, its use is limited by the need for labor-intensive, real-time tracking from a research vessel or the availability of fixed listening stations. Dagorn et al. (2001) described clear interactions between some of the yellowfin tuna (*Thunnus albacares*) being tracked and the research vessel—a violation of the assumption that the tracking operation does not alter the behavior of the fish. Archival tags also collect both environmental and physiological data but

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over much longer time scales (sometimes years) and across ocean-basin geographic scales (Arnold and Dewar, 2001; Gunn and Block, 2001). These tags can provide information on both seasonal behavior and migration routes. Although data collection is fishery-independent, data retrieval is dependent on the recapture of the fish by fishermen and on the recognition and return of the archival tag. PSATs are a merger of archival and satellite telemetry technology. Because PSATs are attached externally, only environmental data can be collected. The tags can be programmed to gather data for a predetermined duration and then to disengage and transmit data at a determined time. The major advantage of this tag is that both data acquisition and retrieval are fishery-independent and the researcher knows when to expect to receive data. However, data retrieval is limited by data compression required to compensate for low data transfer rates to the Argos satellites, finite battery life, and relatively high transmission errors (Arnold and Dewar, 2001; Gunn and Block, 2001). PSATs provide accurate endpoint locations based on Doppler shifts of successive transmissions during a single satellite pass. However, geolocation throughout the tagging duration is based on light levels that estimate dawn and dusk. By determining time of local noon and day length, longitude and latitude can be calculated. According to Hill and Braun (2001), even with optimal geolocation analysis, the expected variability in longitude is a constant  $0.32^\circ$  but the expected variability in latitude will never be less than  $0.7^\circ$ . The relationship between day length and latitude is strongest at high latitudes and at the time of the solstices but weakens near the equator and becomes nearly indeterminate at the equinoxes (Sibert et al., 2003).

An implicit assumption in using these tags is that while the fish tows the tag, the tag does not affect the study animal's behavior or survival. This is a reasonable assumption for large pelagic fishes and is supported by theoretical estimates of the energetic cost of towing a PSAT (Kerstetter, 2002); however, the actual energy cost to a given fish has not previously been quantified. The success of early studies on pelagic fishes has spurred increasing interest in using these tags on a large variety of species and age groups. As studies are undertaken with PSATs, a logical extension is to pose the question: "At what point does the energy cost of carrying a PSAT negatively affect a study animal?" Blaylock (1990) addressed a similar question regarding the impact of sonic transmitters on the swimming behavior of cownose rays (*Rhinoptera bonasus*). In his study, he videotaped cownose rays for ten-minute intervals before and after attachment of a mock transmitter. Energy expenditure was estimated by counting wingbeats per second before and after attachment of the transmitter. He concluded that in the short term a transmitter-to-ray mass ratio of less than 0.03 had no statistically significant effect on ray swimming behavior.

In this study, the impact of a PSAT on a study animal is evaluated in terms of the forces that the PSAT exerts on the animal, specifically lift (i.e., buoyancy)

and drag. Lift and drag are both vector quantities; lift acts in the vertical direction and drag, as measured in this study, acts in the horizontal direction. These vector components are additive to give the total force acting on the attachment site of a PSAT. At a recent tagging workshop associated with the Pelagic Fisheries Research Program,<sup>1</sup> the problem of premature release of some PSATs from the research animal was cited as a common difficulty. Premature release may be attributed to a number of potential failures of either the tag itself or the attachment device. Possible sources for this problem cited at this workshop include detachment of the anchor from the study animal, failure of the tether between the PSAT and the anchor, failure of the release pin on the PSAT, and failure of the release software itself. The magnitude of the total force acting on the attachment site chronically may provide some insight into whether anchor failure is a possible source for this problem.

Drag as an isolated force is the product of four defining factors:

$$F_D = \frac{1}{2} \rho S U^2 C_D, \quad (1)$$

- where  $F_D$  = force due to drag (in newtons, N);  
 $\rho$  = density ( $\text{kg/m}^3$ ) of the fluid through which the object is moving;  
 $S$  = projected surface area ( $\text{m}^2$ ) of the object;  
 $U$  = relative velocity (m/s) between the object and the fluid; and  
 $C_D$  = drag coefficient (dimensionless) which is largely dependent upon the shape of the object.

Furthermore, the power required to pull the tag through the water can also be related to drag mathematically:

$$P = F_D U = \frac{1}{2} \rho S U^3 C_D, \quad (2)$$

where  $P$  = power (in watts, W).

Of particular note in these relationships, drag is proportional to velocity squared and power is related to velocity cubed provided that all other factors are constant. For example, as velocity is doubled, drag increases by a factor of four, whereas power increases by a factor of eight. The characteristic of the tag that most affects drag in this relationship is its projected surface area which, in turn, is defined by its size and shape. The projected surface area of the PSAT changes as the tag is pulled through the water at different velocities and in turn changes the drag coefficient at each velocity. On the other hand, lift is determined by the buoyancy of the tag. The dry weight of the tag is not a factor in either of these relationships under steady flow con-

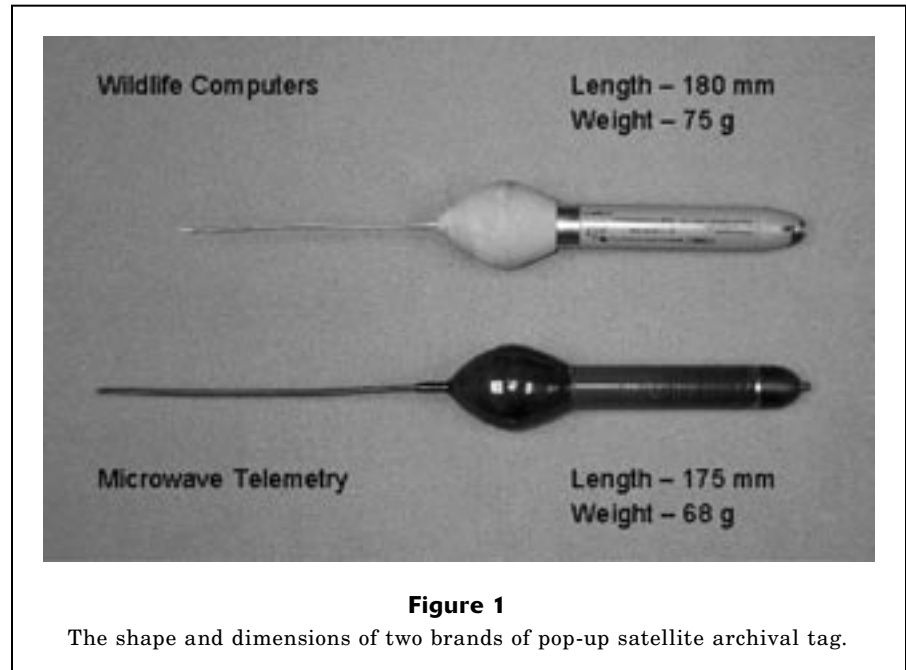
<sup>1</sup> Pelagic Fisheries Research Program. 2002. PFRP PI Meeting, December 4–6, 2002. University of Hawaii at Manoa, 1000 Pope Rd., MSB 312, Honolulu, HI 96822. <http://www.soest.hawaii.edu/PFRP/meetings.html>. [Accessed 16 June 2004.]

ditions. The weight of the tag is only important during accelerations and decelerations. During acceleration, the mass of the tag positively affects the magnitude of two separate forces that add to the hydrodynamic drag, and likewise during deceleration, these extra forces develop on the attachment point that could cause tag loss.

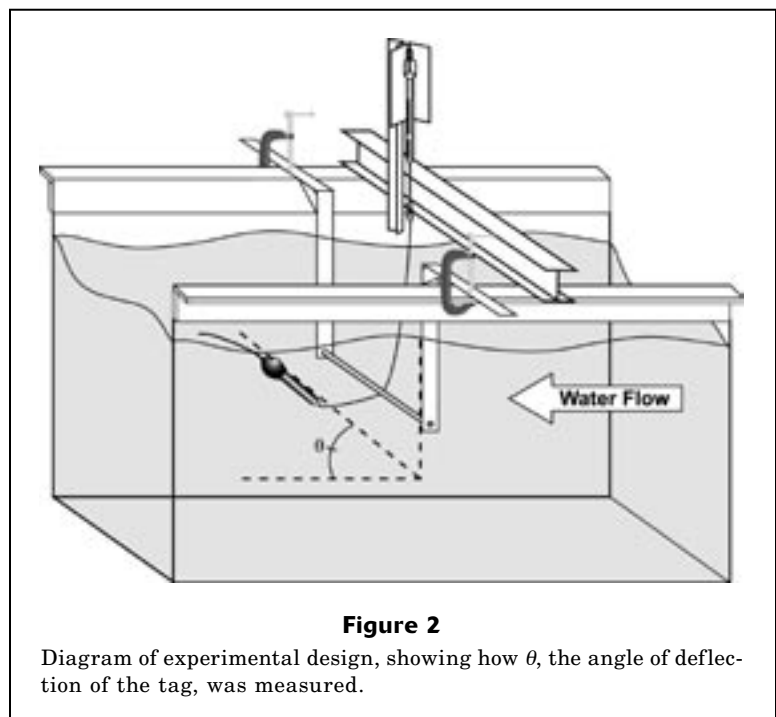
The motivation for this study is to determine the feasibility of tagging cownose rays (*R. bonasus*) with PSATs to study their fall migration. By quantifying the forces that act upon an animal when a PSAT is attached, and using published metabolic rates, we can estimate the energetic cost for the ray to carry a PSAT. Moreover, this type of analysis can be used to determine the minimum size of ray suitable for tagging. Considering the wide variety of user-determined modifications that can be implemented in applying these tags, this experiment is intentionally designed to isolate the PSAT from other variables. In this way, these results can be applied to a broad range of applications so that each user can decide the manner in which a specific modification of the tag is likely to affect the forces of lift and drag.

## Methods

Drag was measured on two brands of PSAT. One tag was manufactured by Wildlife Computers, Inc. (Model PAT, 16150 NE 85<sup>th</sup> St #226, Redmond, WA 98052) and the other was a mock tag made by Microwave Telemetry, Inc. (Model PTT-100, 10280 Old Columbia Road, Suite 260, Columbia, MD 21046) weighted to simulate a functional tag. The two tags are very similar in size and shape (Fig. 1). The Wildlife Computer PAT has a body length of 180 mm (not including the antenna) and a dry weight of 75 g and the Microwave Telemetry PTT is 175 mm long and weighs 68 g. Measurements were obtained in a 22,700-liter freshwater recirculating flume 24 meters in length located at the Virginia Institute of Marine Science. A 30-g spring scale was used to measure force and was suspended above the flume. A 1.25-cm low-friction Delrin rod was suspended approximately 55 cm below the water surface by a metal bracket and placed directly below the spring scale. A 90-cm length of 0.46-mm diameter (20-lb test) monofilament line connected the tag to the spring



**Figure 1**  
The shape and dimensions of two brands of pop-up satellite archival tag.



**Figure 2**  
Diagram of experimental design, showing how  $\theta$ , the angle of deflection of the tag, was measured.

scale by loops tied at either end. One loop was threaded through the release pin in order to lasso the tag. The other loop was then attached to the clip on the spring scale and the tag was passed under the Delrin rod so that it floated to the other side (Fig. 2). The depth of the Delrin rod and the length of the monofilament were selected so that the tag was completely immersed in the water throughout the experiment and so that it floated within

**Table 1**

Spring scale measurements, angle of deflection, summary of forces exerted and power required for two brands of PSAT over flume velocities from 0.00 m/s to 0.60 m/s. The spring scale measurements include the range over a 5-minute period. The angle of deflection was measured from the horizontal. Total force, lift, and drag (in newtons, N) were calculated from Equations 3, 4, and 5, respectively. Power (in watts, W) was calculated as the product of flume velocity and drag.

PSAT	Flume velocity (m/s)	Spring scale measurement (g)	$\theta$ (°)	Total force (N)	Lift (N)	Drag (N)	Power (W)
Wildlife Computers	0.00	6.50 ±0.25	90.0	0.064	0.064	0.000	0.000
	0.15	7.50 ±0.25	76.5	0.074	0.072	0.017	0.003
	0.30	10.50 ±0.25	42.0	0.103	0.069	0.076	0.023
	0.45	15.0 ±0.5	40.0	0.147	0.094	0.113	0.051
	0.60	19.0 ±1.0	31.5	0.186	0.097	0.159	0.095
Microwave Telemetry	0.00	11.75 ±0.25	90.0	0.115	0.115	0.000	0.000
	0.15	12.25 ±0.25	75.5	0.120	0.116	0.030	0.004
	0.30	13.50 ±0.25	61.5	0.132	0.116	0.063	0.019
	0.45	16.0 ±0.5	42.5	0.157	0.106	0.116	0.052
	0.60	21.5 ±1.0	41.5	0.211	0.140	0.159	0.095

the central portion of the flume. Prior to the experiment, the monofilament line was attached to the spring scale and the spring scale was then set at zero so that the weight of the monofilament line was excluded from the subsequent measurements. The flume temperature was measured at 20°C. Measurements were taken on each tag at flume velocities of 0.0, 0.15, 0.30, 0.45, and 0.60 m/s, the maximum velocity of the flume. At each flume velocity, the flume flow was allowed to equilibrate for 10 minutes. Then spring scale measurements were observed over a period of five minutes and the mid-point measurement and its range were recorded. The raw measurement was then converted to total force,  $F_T$  (N):

$$F_T = (\text{raw measurement (g)})(1\text{kg}/1000\text{g})(9.8\text{m/s}^2). \quad (3)$$

In addition, a digital photo was taken of each tag at each velocity from the side of the flume in order to measure the angle of deflection ( $\theta$ ) as measured upward from horizontal. Accordingly, the total force ( $F_T$ ) could then be separated into its component forces, lift ( $F_L$ ) and drag ( $F_D$ ):

$$F_L = \sin \theta F_T, \quad (4)$$

$$F_D = \cos \theta F_T. \quad (5)$$

## Results

The spring scale measurement for the Wildlife Computers PAT increased from 6.50 g at 0.00 m/s to 19.0 g at 0.60 m/s and the Microwave Telemetry PTT increased from 11.75 g to 21.5 g over the same flume velocity increase (Table 1). Because of increasing turbulence

in the flume at the two higher flume velocities, the range of the spring scale measurements also increased. The total force exerted by the Wildlife Computers PAT increased from 0.064 N to 0.186 N as the flume velocity was increased (Table 1). Similarly, the drag and calculated power required to pull the tag through the water column at the highest velocity was 0.159 N and 0.095 W, respectively. The lift of this PSAT also increased, but not continuously, from 0.064 N to 0.097 N. The forces exerted by the Microwave Telemetry PTT were very similar but had higher lift values. The total force increased from 0.115 N to 0.211 N, the drag increased to 0.159 N and the power required to pull this PSAT was 0.095 W at the highest velocity. The lift increased from 0.115 N to 0.140 N but again not in a continuous manner. Force-velocity curves for both PSATs were very similar (Fig. 3). Lift was relatively constant for each tag, although at different magnitudes. Total force and drag both increased over the range of flume velocities and roughly paralleled each other between 0.30 m/s and 0.60 m/s.

## Discussion

Considered alone, the power required to pull a given PSAT at a particular velocity has little relevance, but when considered in the context of an animal's usual energy expenditure to swim at that velocity, it can be expressed as %TAX (Tag Altered eXertion), defined as the increase in energy required by the animal to pull the PSAT at the specified velocity, normalized by the routine or active metabolic rate (see below). In his biotelemetry studies, Blaylock (1992) measured mean routine swimming speeds between 0.20 m/s and 0.29 m/s in cownose rays. Maximum swimming speeds for cownose rays have

not been measured; however, with visual observation, Smith (1980) reported witnessing several undisturbed schools of cownose rays swimming near the surface at ~4–5 knots (2.06–2.57 m/s). Using data reported in first sightings during spring migration of cownose rays along the South Atlantic Bight, Smith estimated migration speeds as high as 12.5 nautical miles per day. Assuming the rays migrated continuously, that rate would require a swimming speed of 0.27 m/s; if they were actively migrating 50% of the time, they would have to swim at 0.54 m/s.

Published metabolic rates can be used to estimate the energy required for an animal to swim at various speeds. When information is not available on a study species, a suitable proxy species can be used. In the example of the cownose ray, no data are currently available regarding metabolic rates; however, DuPreez et al. (1988) published metabolic rates for the bull ray (*Myliobatis [=Myliobatus] aquila*) over a range of temperatures. *Myliobatis aquila* is a good proxy species for *R. bonasus* because the two species are morphologically similar, similar in size, and both inhabit temperate to subtropical coastal waters. Because the flume measurements were obtained at 20°C and this is also a typical mid-range temperature for either species, the equations for metabolic rates at this temperature will be used (Eq. 6, a–c). Metabolic rates are expressed as a set of three equations that yield the standard metabolic rate (SMR), the routine metabolic rate (RMR), and the active metabolic rate (AMR).

$$\begin{aligned} \text{SMR} \quad \log_{10} R &= 2.86 - 0.32 \times \\ &\log_{10} (M \times 1000), \end{aligned} \quad (6a)$$

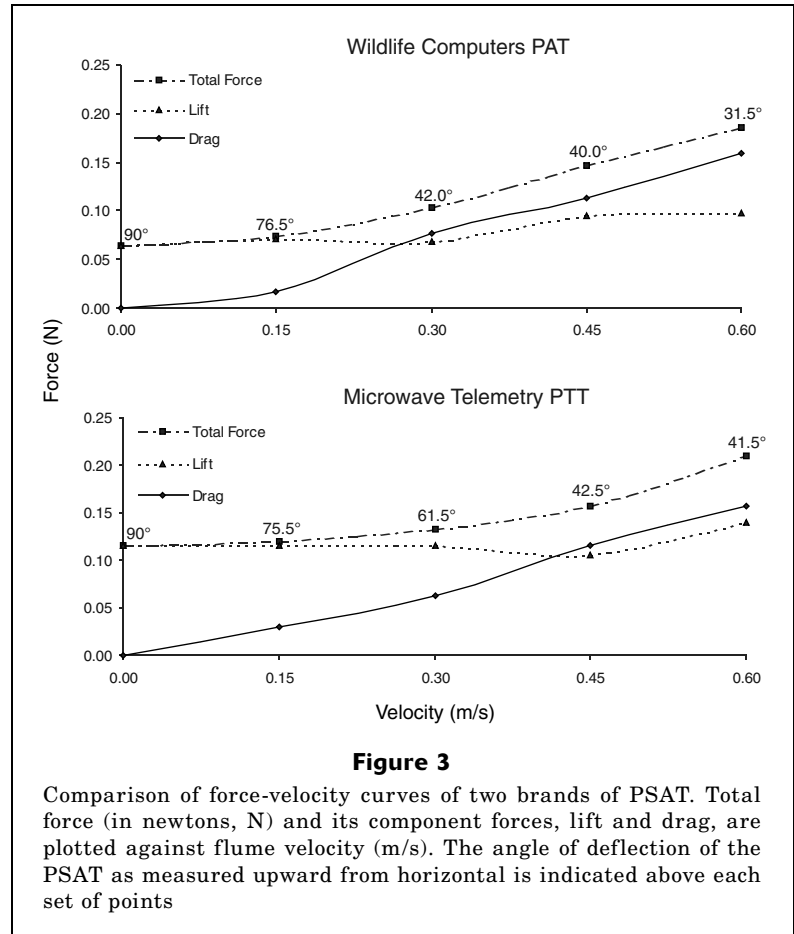
$$\text{RMR} \quad \log_{10} R = 2.79 - 0.27 \times \log_{10} (M \times 1000), \quad (6b)$$

$$\text{AMR} \quad \log_{10} R = 2.74 - 0.22 \times \log_{10} (M \times 1000), \quad (6c)$$

where  $M$  = mass (kg) of the ray (DuPreez et al.'s 1988 equations have been modified so as to express  $M$  in MKS units); and  $R$  = metabolic rate (mg  $O_2$ /(kg  $\times$  h)).

Using the size of an average female cownose ray of 15.5 kg (Smith, 1980) and solving for  $R$ , the SMR, RMR and AMR are estimated as 33.0, 45.6, and 65.8 mg  $O_2$ /(kg  $\times$  h) respectively. These rates can then be used to estimate swimming power at routine and active swimming speeds:

$$\begin{aligned} SP_{2MR} &= (?MR - SMR) \times \\ (1W / \text{kg}) / (256\text{mg } O_2 / (\text{kg} \times \text{h})) \times M, \end{aligned} \quad (7)$$



**Figure 3**

Comparison of force-velocity curves of two brands of PSAT. Total force (in newtons, N) and its component forces, lift and drag, are plotted against flume velocity (m/s). The angle of deflection of the PSAT as measured upward from horizontal is indicated above each set of points

where  $SP_{2MR}$  = swimming power (W) for RMR or AMR.

Making the appropriate substitutions into Equation 7 yields  $SP_{RMR} = 0.76$  W and  $SP_{AMR} = 1.99$  W. Drag can then be expressed as %TAX:

$$\%TAX = (P / SP_{2MR}) \times 100. \quad (8)$$

For swimming speeds of 0.15 m/s and 0.30 m/s,  $SP_{RMR}$  is used, and for swimming speeds of 0.45 m/s and 0.60 m/s,  $SP_{AMR}$  is used (Table 2).

Although lift has not been considered in the above analysis, it is an important component of the total force affecting a study animal. As a chronically applied force acting against the anchor site where the PSAT attaches, this total force may contribute to premature release of the PSAT from the study animal. Moreover, for animals where diving behavior is important for survival (e.g., diving for prey or diving to escape predators) lift becomes an additional tax on the animal's energy resources. Using total force as an approximation of the force to be overcome by the animal when diving, we can estimate the total power required to dive as *Total force as %TAX* (Table 2).

We propose that an increase in energy requirement, %TAX, of <5% will not negatively impact a study ani-

**Table 2**

Metabolic cost to a 15.5 kg cownose ray carrying a PSAT at various velocities expressed as %TAX. Drag and total force are the forces created by the PSAT to be overcome by the swimming ray. Power and total power are the rates of energy expenditure required to overcome these forces. *Drag as %TAX* and *Total force as %TAX* are the increases in energy expenditures, normalized by the routine or active metabolic rate (speed dependent—see text), required to carry the PSAT at a given velocity. Drag, power, and *Drag as %TAX* apply to a ray swimming in the horizontal plane. Total force, total power, and *Total force as %TAX* account for the buoyancy of the PSAT and apply when the ray is diving.

PSAT	Flume velocity (m/s)	Drag (N)	Power (W)	Drag as %TAX	Total force (N)	Total power (W)	Total force as %TAX
Wildlife Computers	0.00	0.000	0.000	0.00	0.064	0.000	0.00
	0.15	0.017	0.003	0.34	0.074	0.011	1.44
	0.30	0.076	0.023	3.01	0.103	0.031	4.05
	0.45	0.113	0.051	2.55	0.147	0.066	3.33
	0.60	0.159	0.095	4.80	0.186	0.112	5.63
Microwave Telemetry	0.00	0.000	0.000	0.00	0.115	0.000	0.00
	0.15	0.030	0.004	0.59	0.120	0.018	2.36
	0.30	0.063	0.019	2.46	0.132	0.040	5.20
	0.45	0.116	0.052	2.62	0.157	0.071	3.55
	0.60	0.159	0.095	4.77	0.211	0.126	6.37

mal that has adequate food resources in nature; higher loads are felt to be energetically significant. In this example using a 15.5-kg cownose ray, the *Drag as %TAX* is within acceptable parameters; however, at 0.60 m/s the *Total force as %TAX* begins to exceed these guidelines. At this point, a researcher would have to consider whether diving behavior at this speed would be a significant factor in the animal's survival.

Another application of this information would be to determine the minimum reasonable size for a study animal of a particular species. Blaylock (1990) attempted to address this issue for cownose rays by considering the transmitter-to-ray mass ratio using dry weights. The advantage of using metabolic rates is that it identifies subtler but significant increases in energy requirement to carry a PSAT. In his study, Blaylock examined two age groups, a 0+ age group that had an average weight of 1.8 kg and a 1+ age group that ranged in size between 4.3 kg and 7.8 kg. He concluded that the 0+ age group was negatively impacted by the sonic tag but that the 1+ age group was not effected. A PSAT is physically smaller than the sonic tags used in his experiment; in addition, it is attached to the animal at the nose-end of the tag so that it is carried with the long axis of the tag parallel to the long axis of the animal (Blaylock's sonic tags were attached so that the long axis of the tag was carried perpendicular to the long axis of the animal). Both these factors—smaller physical size and nose-end orientation in space—decrease the projected surface area of the tag. As an example, consider the metabolic cost of carrying a Wildlife Computers PAT to each of these sizes (1.8, 4.3, and 7.8 kg) of cownose ray (Table 3). For the 1.8-kg ray, only the exertion of carrying the PSAT at 0.15 m/s horizontally was associ-

ated with a %TAX of <5%; higher swimming speeds or downward diving markedly increased the %TAX. It is obvious why short-term effects of carrying a sonic tag were evident. For the 4.3-kg ray, all swimming speeds greater than 0.15 m/s, whether horizontal or diving, required increased energy expenditures of >5%. For the 7.8-kg ray, %TAX was acceptable at 0.15 m/s, marginal to slightly elevated for mid-range speeds, and was clearly excessive at high speed. According to this analysis, rays of these size classes would not be good candidates for carrying a PSAT. As determined in this study, the smallest cownose ray that ought to be considered for PSAT tracking would be 14.8 kg. *Drag as %TAX* is ≤5% for all speeds and only slightly >5% for *Total force as %TAX* at 0.60 m/s. Because prolonged high speed diving behavior is not likely a factor in this ray's ability to survive, the minor elevation of %TAX for diving at 0.60 m/s can be disregarded.

When applying this type of analysis to other species that predominantly swim at speeds greater than 0.60 m/s, several caveats make unwise the extrapolation of these data to higher velocities. Referring back to the equations describing drag and power, Equation 1 and Equation 2, respectively, drag is proportional to velocity squared and power is proportional to velocity cubed provided that all other factors are constant. However, in examining Figure 3, as velocity increases from 0.00 m/s to 0.60 m/s, all other factors are not constant. Specifically, the angle of deflection,  $\theta$ , decreases from 90° at 0.00 m/s to as low as 31.5° at 0.60 m/s. First, the projected surface area,  $S$ , over which water flows decreases as velocity increases. Second, the orientation (effective shape) of the object also effectively changes as velocity increases. Hence the drag co-efficient,  $C_D$

**Table 3**

Metabolic costs to various sizes of cownose ray to carry a Wildlife Computers PSAT expressed as %TAX. Drag as %TAX is the increase in energy expenditure, normalized by the routine or active metabolic rate (speed dependent—see text), required by the ray to carry the PSAT while swimming in the horizontal plane. Total force as %TAX accounts for the buoyancy of the PSAT and applies when the ray is diving.

Weight of ray (kg)	Drag as %TAX				Total force as %TAX			
	Swimming velocity (m/s)				Swimming velocity (m/s)			
	0.15	0.30	0.45	0.60	0.15	0.30	0.45	0.60
1.8	2.39	21.32	18.53	34.84	10.25	28.69	24.19	40.86
4.3	1.05	9.32	8.06	15.16	4.48	12.58	10.53	17.78
7.8	0.62	5.50	4.70	8.84	2.65	7.41	6.41	10.37
14.8	0.35	3.15	2.66	5.00	1.51	4.24	3.48	5.87

also changes. At some velocity greater than 0.60 m/s,  $\theta$  will approach 0°, and at that point  $S$  and  $C_D$  would remain constant for higher velocities. After that velocity is reached, then for higher velocities, drag would increase proportionately to the square of velocity and power would increase proportionately to the cube of velocity. In other words, between 0.00 m/s and 0.60 m/s, the changes in  $S$  and  $C_D$  mask the parabolic relationship of drag with velocity. Because the velocity at which  $S$  and  $C_D$  become constant is not known, extrapolations far beyond the maximum velocity for which drag was measured would be risky.

The effect of the changing values of  $S$  and  $C_D$  is evident in this data set. For example in Table 1, as velocity doubles from 0.30 m/s to 0.60 m/s, drag increases by only 2.09 and 2.52 for the Wildlife Computers PAT and the Microwave Telemetry PTT-100, respectively, rather than by a factor of four. Similarly, power increases by 4.13 and 5.00 for the two PSATs and not by a factor of eight. For both these tags,  $\theta$  decreases with increasing velocity resulting in a smaller value for  $S$  and a different value for  $C_D$ .

By examining the forces exerted by a PSAT at various velocities, insights regarding the impact of these forces on a study animal can be gained. The combined forces of lift and drag act chronically on the anchor site of the PSAT. Although this study does not specifically address attachment methods, the forces of lift and drag exerted by a PSAT are not negligible and cannot be ignored when evaluating an attachment technique. A PSAT also imposes an energetic cost to the study animal. If that energy cost compromises the animal's behavior or survival, the information gained from the tag is not representative of an untagged animal. By estimating the energetic cost to an intended study animal, a researcher can make a more informed decision regarding the suitability of the animal for this type of tagging. Although direct extrapolation to higher swimming speeds is not possible with our data, the principles outlined in this study can be applied to faster swimming species such as tunas and billfishes that are frequently tagged.

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