Optimal diving under the risk of predation

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Abstract

Many air-breathing aquatic foragers may be killed by aerial or subsurface predators while recovering oxygen at the surface; yet the influence of predation risk on time allocation during dive cycles is little known in spite of numerous studies on optimal diving. We modeled diving behavior under the risk of predation at the surface. The relationship between time spent at the surface and the risk of death is predicted to influence the optimal surface interval, regardless of whether foragers accumulate energy at a constant rate while at the food patch, deplete food resources over the course of the dive, or must search for food during the dive. When instantaneous predation risk during a single surface interval decreases with time spent at the surface, a diver should increase its surface interval relative to that which maximizes energy intake, thereby increasing dive durations and reducing the number of surfacings per foraging bout. When instantaneous risk over a single surface interval does not change or increases with increasing time at the surface, divers should decrease their surface interval (and consequently their dive duration) relative to that which maximizes energy intake resulting in more dives per foraging bout. The fitness consequences of selecting a suboptimal surface interval vary with the risk function and the way divers harvest energy when at depth. Finally, predation risk during surface intervals should have important consequences for habitat selection and other aspects of the behavioral ecology of air-breathing aquatic organisms.

1. Introduction

Air-breathing animals that forage underwater represent a diverse array of taxa including insects, fish, amphibians, reptiles, birds, and mammals. These animals engage in diving cycles that consist of time spent at the surface replenishing oxygen stores, time traveling to and from the underwater foraging site, and time spent at the foraging site (Houston and Carbone, 1992). Therefore, they face tradeoffs between gathering energy and replenishing oxygen stores. There have been many theoretical investigations of how animals should allocate time over the course of a single dive cycle or throughout a foraging bout to maximize time spent at the food patch or energy-intake rate, or to select the depth at which to forage (e.g., Kramer, 1988; Ydenberg and Clark, 1989; Houston and Carbone, 1992; Carbone and Houston, 1996; Boyd, 1997; Mori, 1998a, b, 1999; Thompson and Fedak, 2001). In general, increasing time at the surface allows longer dives, and therefore access to deeper prey or more time to feed within a patch.

There is empirical support for some predictions of optimal diving models (review in Boyd, 1997). For example, marbled murrelets (*Brachyramphus marmoratus*) increase surface time as dive time increases (Jodice and Collopy, 1999) and pochards (*Arythya ferina*) increase dive duration and surface time as foraging depth increases (Carbone and Houston, 1994). However, not all studies have found a good match between theory and data. For example, most models fail to explain why some marine birds (e.g., Chappell et al., 1992; Croxall et al., 1993; Jodice and Collopy, 1999) and marine mammals (e.g., Fedak et al., 1988; Thompson et al., 1991; Thompson and Fedak, 2001) perform many dives that are much shorter than their aerobic threshold, and thus could have stayed longer at a foraging patch after a given surface interval. One possible explanation

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for the failure to predict such behavior is that most models assume a simple linear increase in energy intake with time at the foraging depth. Thompson and Fedak (2001) recognized that maximizing time at a foraging depth may not be the only factor influencing diving behavior. Their model suggests that the observed frequency of dives that are shorter than expected based on maximum aerobic capacity may be due to optimal diving and searching behavior when prey are patchily distributed and patches vary in quality. Shallow-diving species were predicted to end dives if they did not encounter prey early in the dive, but the effect was reduced for deep dives. In general, diving patterns of seals support this model (Thompson and Fedak, 2001).

Another hypothesis that might improve the realism of diving models has received little attention; divers may modify their diving behavior to reduce the probability of being killed by a predator. Work by Kramer and colleagues (Kramer and Graham, 1976; Kramer et al., 1983) suggests that air-breathing fishes surface synchronously and modify their surfacing locations to reduce risk from aerial predators. Also, some authors speculate that predation risk from white sharks (*Carcharodon carcharias*) might influence the diving behavior of elephant seals (*Mirounga angustirostris*) departing from and arriving at haul-out sites (Le Boeuf and Crocker, 1996), and that shallow dive angles in green turtles (*Chelonia mydas*) may improve predator detection (Glen et al., 2001). There have been no theoretical or empirical attempts, however, to understand how predation risk influences the allocation of time over individual dive cycles, or over the series of dives that comprise a foraging bout.

Risk of predation is likely important in the behavioral ecology of diving animals for several reasons. First, almost all species—terrestrial and aquatic alike—employ a diverse array of anti-predator behaviors to reduce the probability of encountering or being captured by a predator. Many species increase their level of vigilance and reduce their movement and foraging rates in response to the presence of predators or the probability of encountering a predator (e.g. Brown et al., 1999; Hamilton and Heithaus, 2001; see Lima and Dill (1990) and Lima (1998) for reviews). Furthermore, many species select safer habitats at the cost of lower rates of energy intake (Abrahams and Dill, 1989; McNamara and Houston, 1990; Grand and Dill, 1997; Heithaus and Dill, 2002), and may forage in a manner that minimizes the probability of death (μ) divided by energetic gains while foraging (G) (e.g. creek chub, *Semotilus atromaculatus*, Gilliam and Fraser, 1987).

Second, many diving animals face the risk of being killed by subsurface predators, aerial predators, or both. For example, seabirds resting on the ocean surface (Dekker and Bogaert, 1997) and air-breathing fishes surfacing to breathe (Kramer and Graham, 1976) face aerial predators. When risk is limited to aerial predators, the surface generally will be the only dangerous part of a dive cycle (exceptions might be when aerial predators plunge to attack a submerged diver; also see Kramer et al., 1983). Although subsurface predators might attack divers at any point during the dive cycle, risk from subsurface predators often appears to be highest while foragers are at the surface potentially due to the following mechanisms. First, scanning of the underwater environment is mutually exclusive with breathing for the period when divers (except cetaceans and sireneans) bring their head, and thus eyes, out of the water. Second, even with the head submerged, a diver at the surface looking towards deeper parts of the water column has poorer visual detection due to reduced light at depth (Strong, 1996), and in some cases predators may be cryptic against the bottom (e.g. Heithaus et al., 2002b). Third, there are fewer escape directions because a diver at the surface can only flee laterally or downwards (Strong, 1996; Heithaus et al., 2002b). Subsurface predators, particularly sharks and killer whales (*Orcinus orca*) are important to many marine mammals, birds, and reptiles (e.g. Ainley et al., 1981; Le Boeuf et al., 1982; Jefferson et al., 1991; Heithaus, 2001a). For instance, tiger sharks (*Galeocerdo cuvier*) in Western Australia frequently attack sea turtles and bottlenose dolphins (*Tursiops aduncus*) (Heithaus, 2001b; Heithaus et al., 2002a), and also prey on other divers, including dugongs (*Dugong dugon*), sea snakes, and sea birds (Heithaus, 2001b; Simpfendorfer et al., 2001). Teleosts may be important predators of small-bodied divers in freshwater and marine habitats.

The goal of this paper is to develop a general framework for understanding the influence of predation risk on diving behavior of air-breathing aquatic animals. We investigate how animals should modify their allocation of time over the dive cycle (i.e., surface intervals and resulting time spent at the food patch) when faced with the risk of predation while at the surface. We consider situations in which divers forage for either a fixed time interval or until reaching a critical energy threshold (e.g., to fill gut capacity). For both situations, we investigate the effects of a linear increase in cumulative energy intake with time at the foraging patch, as well as energy-intake functions that include search times and patch depletion. Within these six diving scenarios, we consider three ways in which the instantaneous risk of predation may interact with time spent at the surface during a single surfacing event: unchanging instantaneous risk (UIR), increasing instantaneous risk (IIR), and decreasing instantaneous risk (DIR).

2. A graphical model of dive cycles

We begin by asking how a diver under predation risk should organize its dive cycle such that it increases

safety at the surface, while continuing to optimize time at the foraging patch. We address this question using the marginal value theorem approach of Kramer (1988), where divers at the surface replenish oxygen stores at a decelerating rate. The optimal surface time (s^*) can be determined by drawing a line tangential to this function from the travel time to and from the bottom (τ) (Fig. 1). If a diver faces predation risk while replenishing oxygen stores, it may reduce risk over the course of an individual dive cycle by shortening its surface interval (i.e., shift from s^* to s_r^*: Fig. 1). As a result, during the next dive, the forager would have to shift to a shorter travel time (i.e., choose a shallower food patch and shift from τ to τ_r: Fig. 1) or otherwise dive inefficiently. However, shorter surface intervals may not necessarily reduce predation risk over the course of a foraging bout. In fact, they might increase the overall risk by shortening dive durations and therefore increasing the number of potentially dangerous surfacings. We expected that optimal surface intervals would differ between situations in which instantaneous predation risk increases, decreases, or remains at the same level with increasing time spent at the surface during a single surfacing event. The following model explores this hypothesis.

3. An analytical model of foraging bouts

A diving forager faces risk of predation while at the surface. It may alter its energy intake and predation risk by modifying surface interval duration and resulting time at the food patch. The diver uses a pure tactic; it
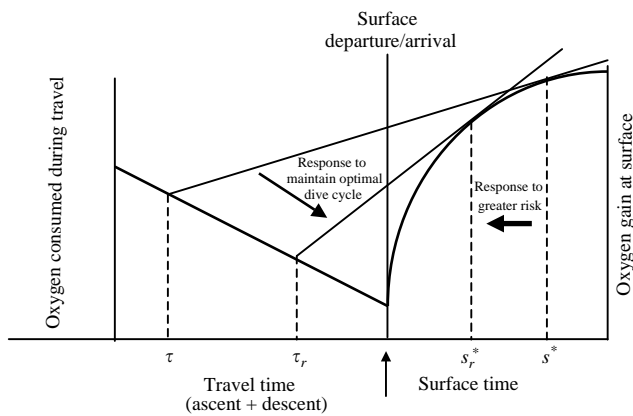

Fig. 1. Graphical model that incorporates predation risk into Kramer's (1988) model of optimal time allocation during a dive cycle. The vertical arrow on the *x*-axis marks the moment of either arriving at or departing from the surface. To the right of the arrow, time at the surface increases and the diver experiences an oxygen gain curve with diminishing returns. To the left of the arrow, time traveling to and returning from the foraging patch (ascent and descent) increases, and so does oxygen consumed while traveling. When there is predation risk, the diver chooses a shorter surface period, s_r^*, which has the cost of a shorter dive and travel time, τ_r.

selects a single surface time (with resulting time at the food patch) that it uses throughout the foraging bout. Thus, the diver selects the optimal surface interval for minimizing $\mu/G\,(s_r^*)$ over the course of a foraging bout. Empirical studies have shown that divers adaptively modify their diving behavior in response to changes in prey abundance (e.g., Antarctic fur seals, *Arctocephalus gazella*, Boyd et al., 1994) and to the risk of predation (e.g., air-breathing fishes, Kramer and Graham, 1976; Kramer et al., 1983), making this a reasonable currency for diving decisions.

Table 1 summarizes parameter values representing a range of risk levels and shapes of risk functions. The net energy gain (G) for a single dive is determined by the amount of energy gained while at the food patch (E) and that expended throughout the dive cycle. If τ is travel time (descent plus ascent), b is time at the food patch, s is the time at the surface, and C_τ, C_b, and C_s represent the metabolic costs per unit time of travel, foraging, and time at the surface, respectively, then

$$G = E - \tau C_\tau - b C_b - s C_s. \qquad (1)$$

We make the simplifying assumptions that (a) travel time relates directly to diving depth, (b) travel and

Table 1
Parameters and values used in the model

Parameter	Symbol	Units	Value
Foraging time available	T	s	50,000
Surface time	s	s	1–450
Travel time	τ	s	10–210
Travel cost	C_τ	Energy/s	0.0001
Foraging cost	C_b	Energy/s	0.00005
Surface cost	C_s	Energy/s	0.000001
Energy-intake rate	I	Energy/s	0.01
Search-time scaling coefficient	θ		2
Search-time scaling coefficient	φ		10,000
Depletion scaling coefficient	λ		0.0007
Maximum energy intake/dive	M	Energy	2
Maximum food patch time	K	s	240
Food patch-time scaling coefficient	α		0.025
Predation risk	r	Probability/s	$10^{-2}, 10^{-3}, 10^{-5}, 10^{-7}$
Predation risk scaling coefficient	β		1.5, 2.0, 3.0, 4.0
Predation risk scaling coefficient	δ		10^8
Predation risk scaling coefficient	γ		0.05, 0.025, 0.005
Maximum risk/surfacing	R	Probability	$10^{-2}, 10^{-3}, 10^{-5}, 10^{-7}$
Critical energy intake	G_{crit}	Energy	5, 20, 40, 60

foraging costs per unit time are fixed, and (c) only one foraging depth is chosen for a particular foraging bout.

We make three different assumptions about how a forager gains energy once at the food patch. In the first, search time is not required (energy gain begins upon arrival) and patches do not deplete (intake rate is constant) such that

$$E = bI, \tag{2}$$

where I is the energy intake per unit time.

In the second assumption, there is an accelerating function of energy intake with time at the food patch because foragers must search before beginning to harvest resources. Therefore,

$$E = \frac{b^\theta}{\varphi}, \tag{3}$$

where θ and φ are scaling coefficients.

Third, if food resources deplete during a dive, energy intake will be a decelerating function that can be modeled as

$$E = M(1 - e^{-\lambda b}), \tag{4}$$

where M is the maximum energy gain while at the food patch and λ is a scaling coefficient. These energy-intake functions do not incorporate the behavior of the diver's prey, nor apply to single-prey loaders, which return to the surface upon capturing a prey item. Therefore, these functions apply most realistically to divers that forage on relatively immobile prey such as benthic invertebrates, seagrass, krill, or algae. However, over the course of a foraging bout, these energy gain functions can be considered as energy-intake probabilities, and thus predictions about average surface intervals under the risk of predation relative to a no-predation risk scenario are still valid.

Time at the food patch (b) can be mathematically expressed in terms of surface time (s) as

$$b = K(1 - e^{-\alpha s}) - \tau, \tag{5}$$

where K is the maximum time at the food patch achievable with aerobic respiration and α is a scaling coefficient. Eq. (5) makes the simplifying assumption that foragers will spend the maximum amount of time at the food patch for a given surface interval without shifting to anaerobic metabolism.

We consider three different ways in which instantaneous predation risk relates to the time a diver spends at the surface during a single surfacing event: unchanging (UIR), increasing (IIR), and decreasing (DIR) functions. The simplest situation is UIR where the probability of death per unit time (r), or instantaneous predation risk, does not change with time spent at the surface. This situation might occur when predation risk is influenced primarily by encounter rates with predators

and divers cannot reduce risk through vigilance at the surface or shortly before surfacing. The cumulative probability of predation over the duration of a single surfacing event (μ_1) can thus be represented with the equation

$$\mu_1 = 1 - (1 - r)^s, \tag{6}$$

where r is the risk per unit time at the surface. The cumulative probability of being killed by a predator over an entire foraging bout (μ_T) is

$$\mu_T = 1 - (1 - \mu_1)^N, \tag{7}$$

where N is the number of dives made over the foraging bout. N will be determined by the time available to forage (T), the surface time selected by the diver, and the travel time to the foraging patch. We make two sets of assumptions about how a diver will forage. In the first situation, we assume that a diver forages for a fixed period of time over which it must optimize its energy intake balanced with the risk of death from predators. The forager cannot reduce its time spent under the risk of predation by foraging for less time, but may modify its probability of death by changing its diving behavior. Thus,

$$N = \frac{T}{b + \tau + s}. \tag{8}$$

In the second situation, a forager remains in the foraging area only until it reaches a net energy-intake threshold (G_{crit}, e.g. a gut-capacity constraint). After that time, we assume that the forager leaves the area and is no longer threatened by predators. Therefore, the number of dives made is represented by

$$N = \frac{t}{b + \tau + s}, \tag{9}$$

where t is the amount of time required to reach G_{crit}.

When subsurface predators threaten divers, risk might be relatively low when they first surface to breathe if they can be vigilant as they approach the surface. However, once at the surface, the instantaneous risk of predation would increase, as a diver cannot be vigilant for subsurface predators while breathing and its eyes are out of the water. The increase in risk with increasing time spent at the surface (Fig. 1a) is represented by

$$\mu_1 = \frac{s^\beta}{\delta}, \tag{11}$$

where β and δ are scaling coefficients. The cumulative probability of being killed by a predator (μ_T) is calculated using Eq. (7) (Fig. 1b).

In some situations, the instantaneous risk to a diver may decrease with increasing time at the surface. For example, a diving seabird at risk from an aerial predator may have relatively high risk upon surfacing if it cannot determine if there is a predator present, but may then face a lower instantaneous risk of death because it can

be vigilant while breathing. In some situations, the cumulative risk may reach an asymptote, as a diver may be able to detect predators at a sufficient distance to take evasive actions. Therefore,

$$\mu_1 = R(1 - e^{-\gamma s}), \tag{12}$$

where R is the maximum cumulative risk that a forager may face during a foraging bout and γ is a scaling coefficient (Fig. 1a). The cumulative probability of being killed by a predator (μ_T) is calculated using Eq. (7) (Fig. 1b).

We use the parameters listed in Table 1 and the above equations to determine the surface time (s_r^*) that optimizes time at the foraging patch and safety over a variety of travel times and for all combinations of the three energy-intake functions, two foraging scenarios, and three predation risk regimes outlined above. As a surrogate of fitness, we assume divers minimize the value of μ/G over the course of a foraging bout. Thus, the optimal surface time is represented by

$$s_r^* = \min_s \left[\frac{\mu_{Ts}}{N_s G_s} \right]. \tag{13}$$

We then compare values of s_r^* to the predicted surface intervals that would maximize the net energy gain, were the predation risk ignored (s^*).

4. Results

4.1. Fixed foraging time

How risk of predation affects surface interval depends upon the relationship between predation risk and surface time (Figs. 2–4). In general, in situations with UIR or IIR, the surface interval that optimizes safety and energy intake, s_r^*, is shorter than the surface interval that would maximize energy intake or time at the prey patch, s^*. With UIR, divers choosing surface intervals longer than s_r^* achieve diminishing energetic returns, while the risk of death increases in an almost linear fashion (Figs. 2a, 3a and 4a). Under conditions of IIR, s_r^* should be much shorter than s^*. Although a forager must make more numerous and less-efficient dives, the forager is exposed to very little risk (Figs. 2b, 3b and 4b). With DIR, s_r^* is longer than s^* because the longer surface interval increases dive duration and decreases the number of high-risk periods that occur upon each surfacing (Figs. 2c, 3c and 4c).

The shape of the energy-intake function does not qualitatively change the above results. However, the magnitude of the difference between s_r^* and s^* depends on how energy is harvested, especially when foragers must search for prey (Fig. 5). In general, the addition of a search time increases the difference between s_r^* and s^*,

while depletion decreases the difference relative to a linear energy-intake function.

Travel time (τ) strongly affects s_r^*, but the shape of the relationship depends partially on the energy-intake function. As with previous models (e.g., Kramer, 1988), our model predicts an increase in surface interval with increasing travel time in almost all situations, but there is no influence of travel time on the *direction* of a diver's surface time modification when faced with the risk of predation (Fig. 5). With a linear increase in energy intake, there is no change with τ in the magnitude that foragers should reduce or increase their surface interval relative to that which maximizes energy intake. With depletion, the magnitude of change in the surface interval increases as travel time increases most notably in the case of decreasing risk. In fact, there is very little difference between s_r^* and s^* when travel times are relatively short. When foragers must search for prey, there is slightly less shift in optimal surface times as travel time increases.

Assuming that μ/G is an indirect measure of fitness (i.e., fitness is influenced by both longevity and energy gain per bout of diving), both the relationship between predation risk and surface time and that between energy intake and time at the food patch influence the fitness consequences of suboptimal decisions regarding surface time (Fig. 6). In general, there is a steep fitness function associated with IIR, regardless of the energy-intake function, and there would be relatively large costs to selecting surface intervals that deviate from s_r^*. Under UIR conditions, there would be a large cost to shifting to a surface interval shorter than s_r^*, primarily due to reduced energy intake rather than increased susceptibility to predators. Shifting to a surface interval longer than s_r^* is less costly, with the fitness cost dictated by the energy-harvesting function. There is a greater cost to surfacing for intervals greater than s_r^* when energy intake is linear than if there is patch depletion or foragers must search for food. A DIR function has large fitness consequences of shifting to a very short surface interval, but there is a large range of longer than optimal surface intervals for which there is very little change in μ/G (Fig. 6).

The costs to energy intake incurred by a diver that chooses s_r^* rather than s^* can be influenced by travel time, the energy-intake function, and the predation risk function (Fig. 7). In general, when divers face UIR, relatively little energy is lost by choosing s_r^* rather than s^*. However, a diver may realize a substantially reduced energy intake with IIR, particularly when travel times are small and foragers must search for prey.

4.2. Fixed energy requirement

The results for divers foraging to meet a fixed energy requirement are similar to those obtained
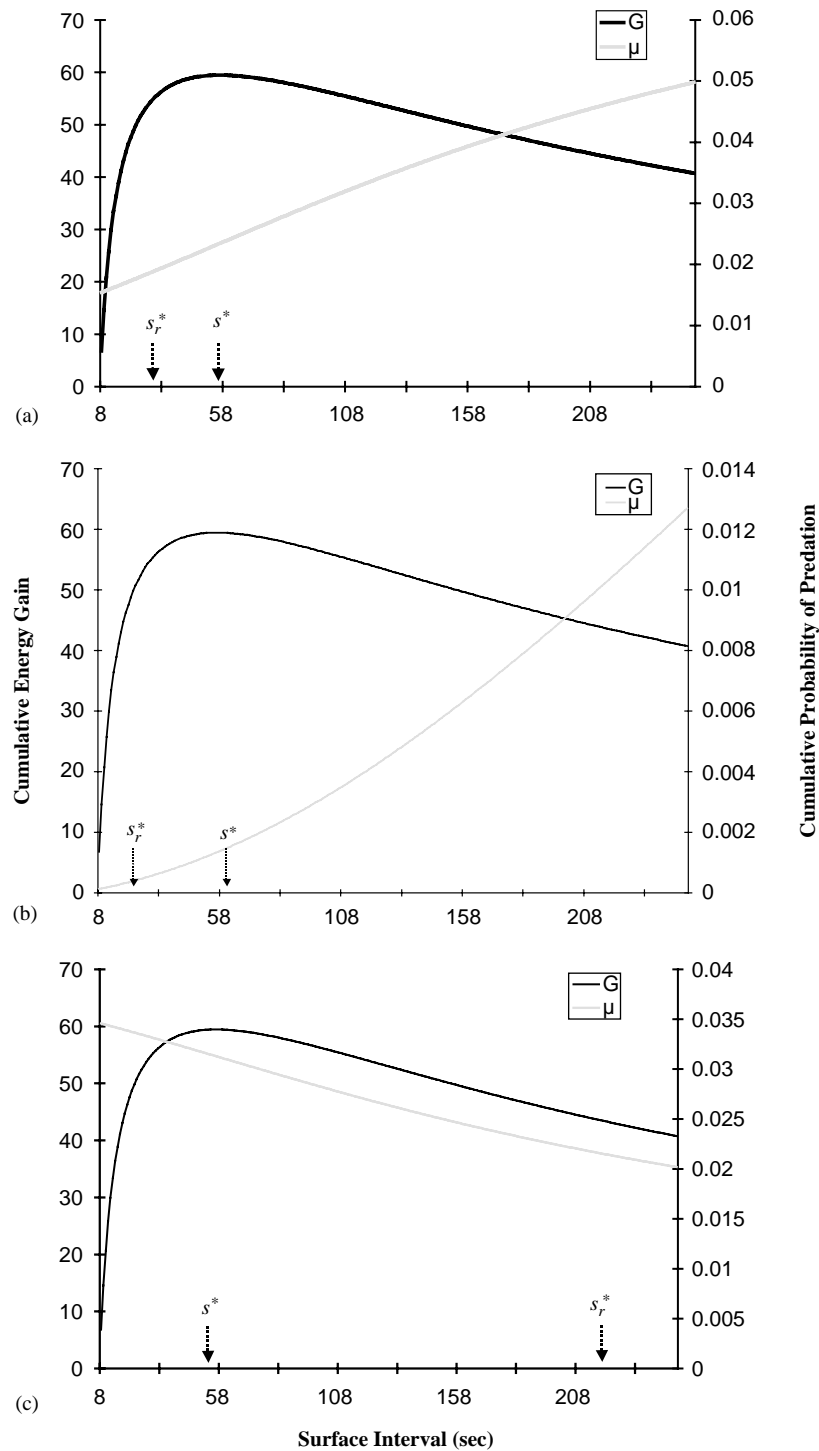
Fig. 2. Influence of surface interval on net energy intake and the cumulative probability of being killed by a predator when energy intake increases linearly with time at the food patch when foraging time is fixed. (a) UIR, (b) IIR, (c) DIR; $\tau = 40$. (a) $r = 10^{-5}$, (b) $\beta = 3.0$, (c) $\gamma = 0.025$.

for a fixed foraging time (compare Figs. 5 and 8). In fact, with UIR, s_r^* is the same for both foraging scenarios regardless of the energy-intake function. There is also very little difference in s_r^* with IIR. The most noticeable difference occurs for DIR. When energy intake is linear, there is a smaller difference

between s_r^* and s^* compared to the fixed foraging time situation, especially when travel time is short (Fig. 5a and 8a). When there is resource depletion and DIR, results are similar for both foraging scenarios at low travel times. However, as travel time increases, divers foraging to reach an energetic intake goal rapidly
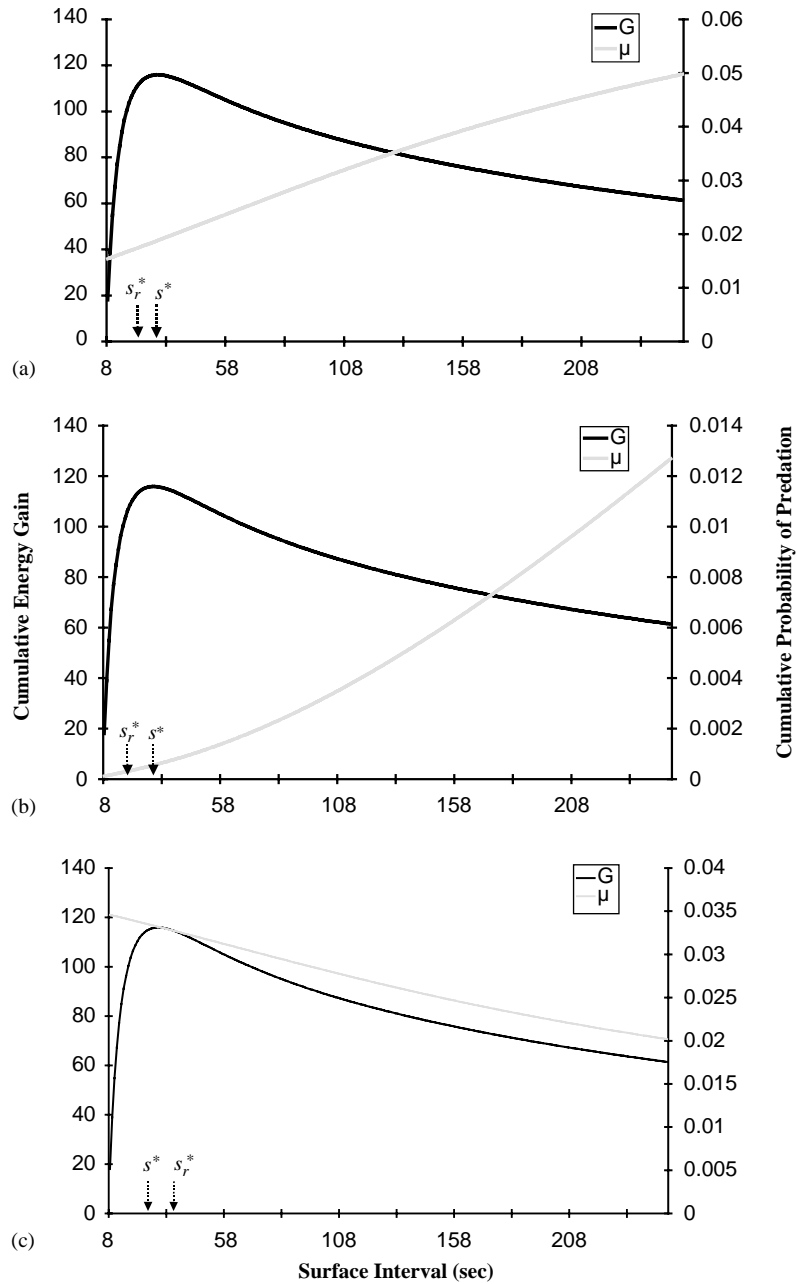
Fig. 3. Influence of surface interval on net energy intake and the cumulative probability of being killed by a predator with search time when foraging time is fixed. (a) UIR, (b) IIR, (c) DIR; $\tau = 40$. (a) $r = 10^{-5}$, (b) $\beta = 3.0$, (c) $\gamma = 0.025$.

switch to the longest possible surface interval that still allows the energy requirement to be met within the foraging period. When there is a search time, a diver immediately begins foraging at the maximum possible surface interval because long surface intervals and resulting long food patch times are beneficial for both reducing overall risk and increasing energetic intake.

When the foraging requirement is relatively high, s_r^* does not always result in animals achieving their energy requirement within the specified time period. In this situation, divers should select the shortest (UIR, IIR) or

longest (DIR) possible surface interval that allows them to achieve the energy requirement.

The fitness consequences of suboptimal decisions regarding surface time are somewhat similar to those for the fixed foraging time model (Fig. 9). However, there is a smaller fitness consequence to shifting the surface interval above s_r^* for IIR functions when there is resource depletion over the course of a dive or a search time to find resources during each dive. Conversely, with UIR, there is a greater fitness consequence to having a surface interval longer than s_r^* for all energy-intake functions.
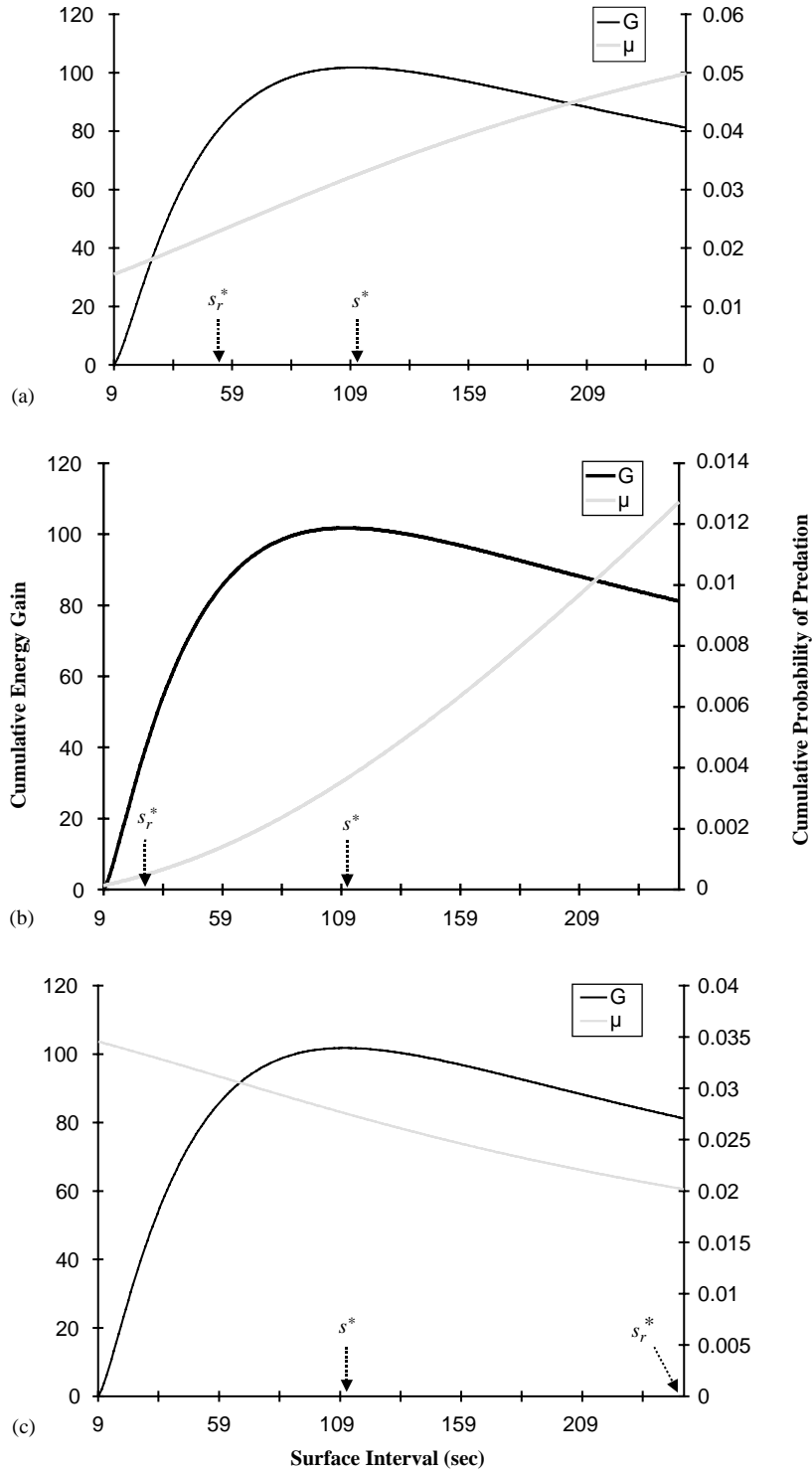
Fig. 4. Influence of surface interval on net energy intake and the cumulative probability of being killed by a predator with depletion when foraging time is fixed. (a) UIR, (b) IIR, (c) DIR; $\tau = 40$. (a) $r = 10^{-5}$, (b) $\beta = 3.0$, (c) $\gamma = 0.025$.

4.3. Scaling coefficients

Because of the assumption that foragers attempt to minimize μ/G, changes in parameters that only influence the absolute level of risk (i.e., R, δ,) have no effect on the optimal surface time under any circumstances. How-

ever, the optimal surface time is influenced by scaling coefficients that change the shape or slope of the predation risk—surface interval function. When the value of r is very high (i.e., very dangerous; e.g., 0.001), the optimal surface interval to minimize μ/G becomes the same as that for maximizing energy-intake rate
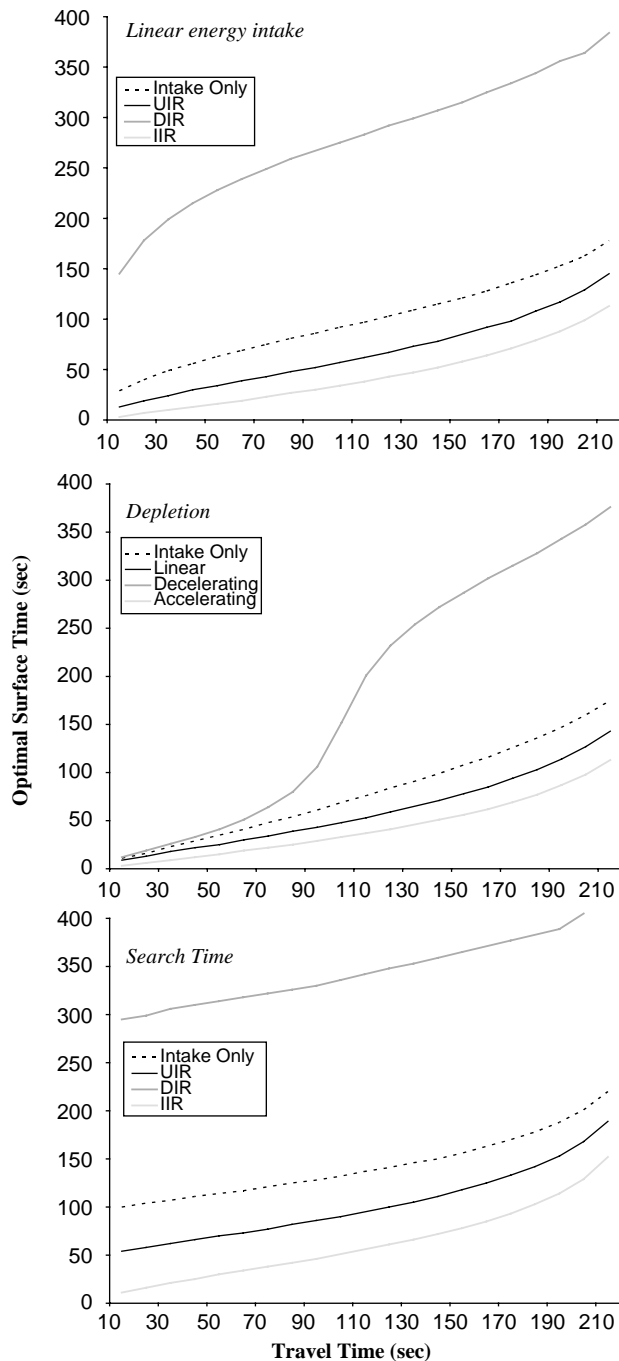
Fig. 5. Influence of travel time on the optimal surface interval under various energy-intake functions and predation risk functions when a diver forages for a fixed period of time. (a) Energy harvested at a constant rate, (b) depletion of a patch over a foraging dive, and (c) search time required to begin harvesting resources. $r = 10^{-5}$, $\beta = 3.0$, $\gamma = 0.025$.

faster acceleration of the risk function and foragers should shift to even shorter surface intervals in order to take advantage of the low-risk portion of the surface interval and avoid the period of high instantaneous predation risk. Surface intervals are also influenced by changes in γ, with lower values resulting in shorter surface intervals as the DIR cumulative predation risk curve becomes more linear.

5. Discussion

Our model predicts that divers at risk of predation, while at the surface, should modify their surface interval to reduce their probability of death during a foraging bout. If instantaneous predation risk does not change, or increases, with time spent at the surface during a single surface interval (UIR and IIR respectively), the optimal surface interval is shorter than the interval that would maximize energy intake, particularly in an IIR situation. An IIR function may apply to divers threatened by submerged predators. For example, sea turtles threatened by sharks cannot be vigilant when breathing, but could assess subsurface risks during ascent. UIR may be less common, but could occur when a small-bodied diver faces risk from the subsurface and aerial predators concurrently and vigilance must be divided above and below the surface.

Our model predicts that foragers facing DIR at the surface should surface and dive for longer periods than those that would maximize energy intake in the absence of predation risk. This situation most likely occurs for divers at risk only from aerial predators. Because visibility through the air is good and most divers can escape aerial predators by diving or flying away, risk is probably low once a diver at the surface can begin to monitor its surroundings.

The above predictions hold regardless of travel time, energy-intake function, or foraging scenario. However, the magnitude of a diver's response to predation risk is influenced by all of these factors and the fitness consequences of a suboptimal surface interval may be greatly influenced by the energy-intake function. Therefore, divers in different habitats or that forage on different types of prey (e.g., benthic grazers vs. pelagic foragers feeding on schooling fish) may show different magnitudes of response to the same predator or type of predation risk.

Divers that change their behavior in response to predators realize lower energy-intake rates, but the magnitude of this cost depends on the energy-intake and risk functions, as well as the foraging depth (i.e., travel time). This reduced energy intake is likely to have important ecological consequences. For example, it may make some habitats unusable if energy intake falls below a critical threshold.
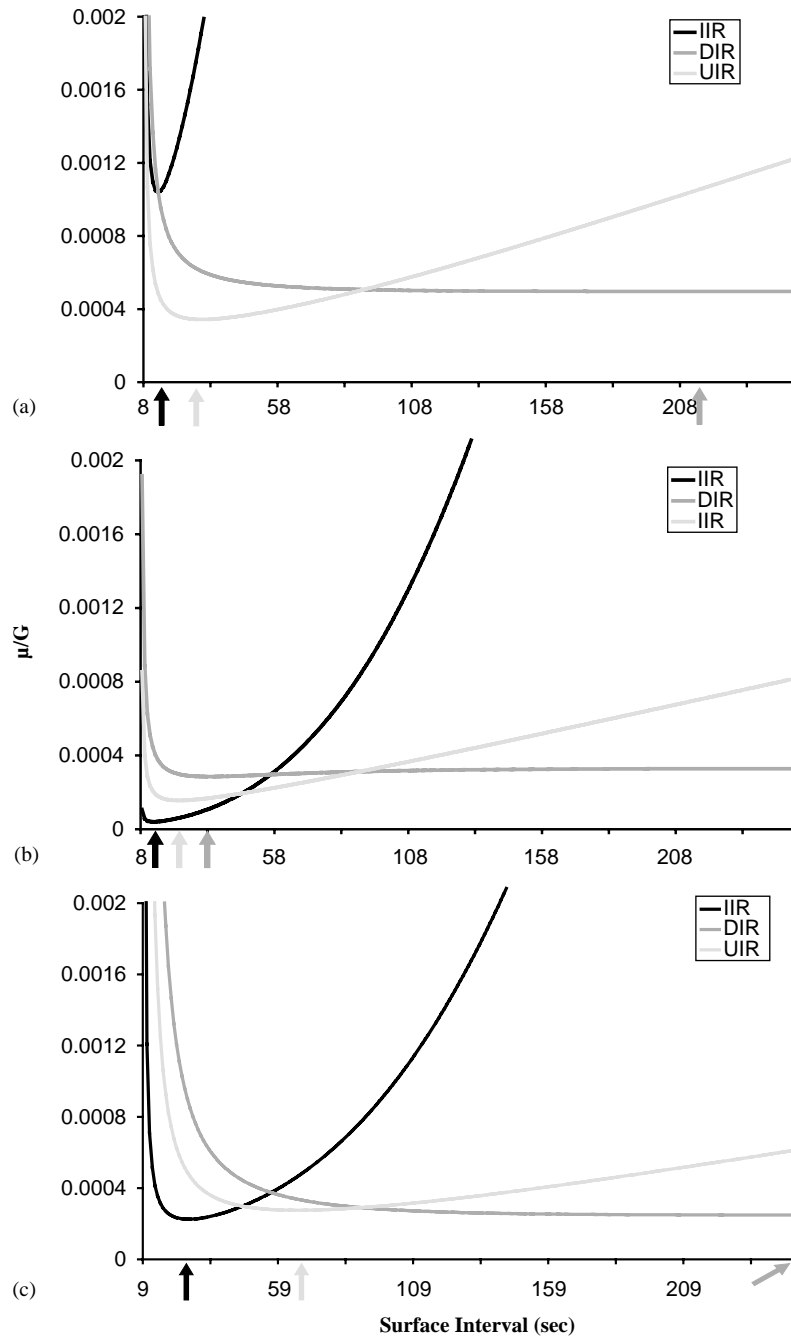
because there is strong selection to minimize the total time spent at the surface regardless of the rate of energy intake. However, as the value of r drops to a more realistic level, a diver should reduce its surface interval relative to the optimum for energy intake. Changes in β follow an opposite pattern. As β increases, there is a

Fig. 6. Influence of surface interval on μ/G when a diver forages for a fixed period of time. Arrows denote s_r^*. Note the different consequences for selection of a suboptimal surface interval. (a) Energy harvested at a constant rate, (b) depletion of a patch over a foraging dive, and (c) search time required to begin harvesting resources. $\tau = 40$, $r = 10^{-5}$, $\beta = 3.0$, $\gamma = 0.025$.

We are unaware of empirical studies that provide adequate data to test all the predictions of this model. Most studies of diving animals look for a positive relationship between travel time (or water depth) and surface time, or between dive time and surface time, and our model predicts that these qualitative relationships will remain intact in most foraging and risk situations. Quantitative field and experimental studies in the future should be able to test our model predictions. In the laboratory, perceived risk (e.g., predator models

or odor cues) could easily be manipulated and differences in diving behavior measured between risk and no-risk treatments. In the field, studies could use spatial or temporal variation in predation risk as treatments. For example, current studies of diving behavior by loggerhead turtles (*Caretta caretta*) during periods of high and low abundance of tiger sharks suggest a qualitative fit to some of our model predications (Frid, Heithaus, Dill, unpublished data). During periods of high tiger shark abundance, loggerhead turtles
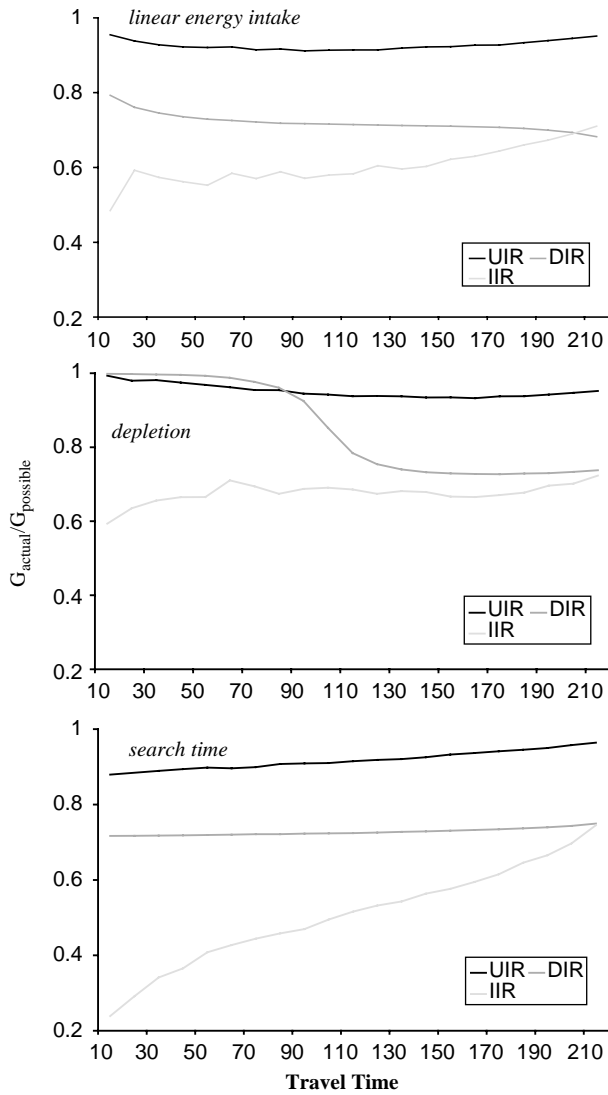
Fig. 7. Proportion of total possible energy intake (if divers select s^*) consumed by foragers that dive using s_r^*. $r = 10^{-5}$, $\beta = 3.0$, $\gamma = 0.025$.

surfaced briefly relative to periods of low tiger shark abundance when turtles had longer surface and dive times.

5.1. Implications for aquatic habitat selection

So far we have addressed how a diver should modify its surface interval based on a tradeoff between energy intake and predation risk. This tradeoff likely has important consequences for habitat use. Our graphical model (Fig. 1) suggests that a diver under the risk of predation during a single dive should shorten its surface interval and select a shallower foraging patch for the subsequent dive. In the analytical model (Figs. 2–9), if all depths (represented by differences in travel time, τ) are available to a diver and are identical in predation risk and food availability, the diver should always shift
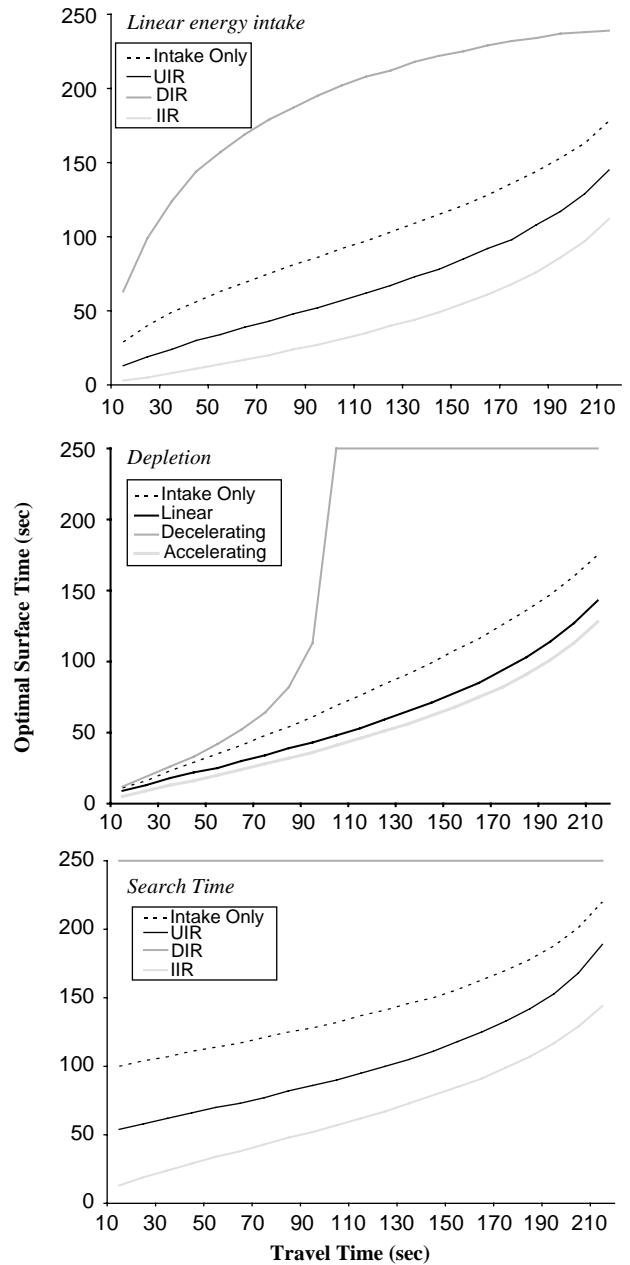

Fig. 8. Influence of travel time on the optimal surface interval under various energy-intake functions and predation-risk functions when a diver forages to meet an energy requirement. (a) Energy harvested at a constant rate, (b) depletion of a patch over a foraging dive, and (c) search time required to begin harvesting resources. $r = 10^{-5}$, $\beta = 3.0$, $\gamma = 0.025$.

to the shallowest habitat in order to minimize travel time and thus maximize time at the foraging patch while minimizing time at the surface. However, all depth possibilities may not be available to a diver, and habitats (or depths) often differ in food availability, which can alter this predicted habitat choice. For example, pochards will shift into deeper habitats to forage if food availability is higher than in shallow ones
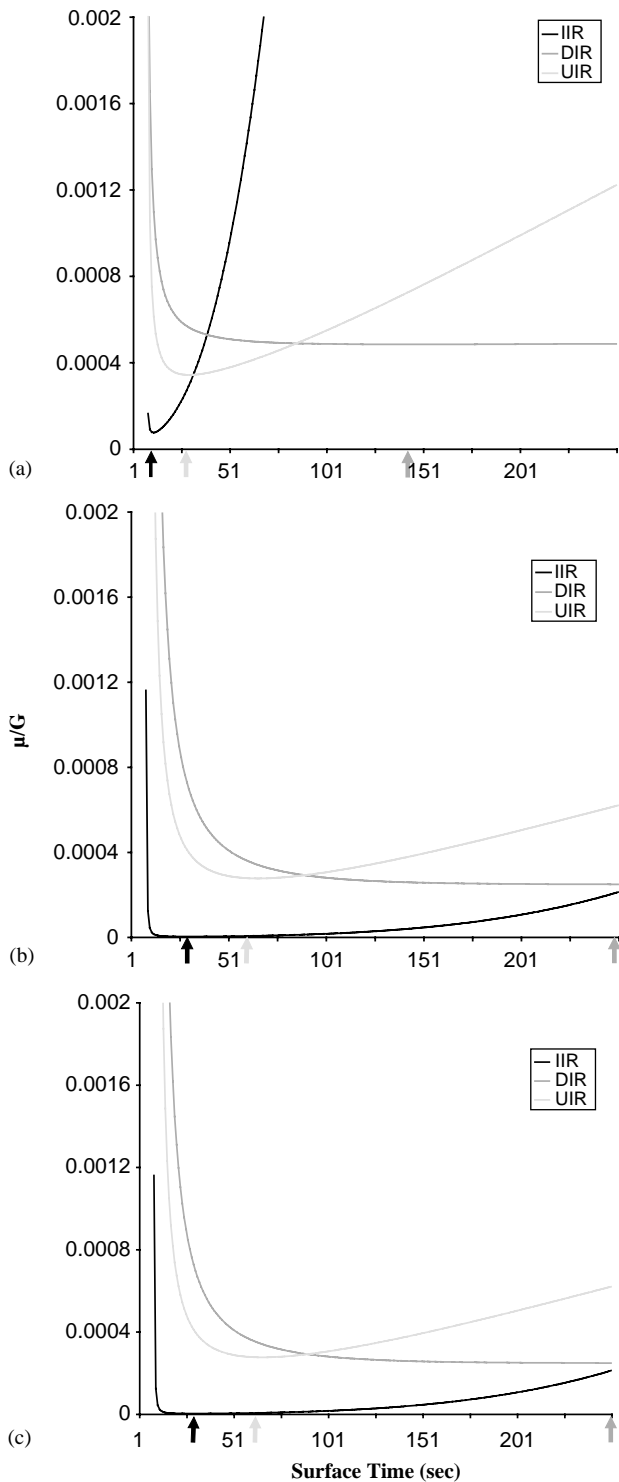
Fig. 9. Influence of surface interval on μ/G when a diver forages to meet an energy requirement. Arrows denote s_r^*. Note the different consequences for suboptimal selection of a surface interval. (a) Energy harvested at a constant rate, (b) depletion of a patch over a foraging dive, and (c) search time required to begin harvesting resources. $\tau = 40$, $r = 10^{-5}$, $\beta = 3.0$, $\gamma = 0.025$.

(Carbone and Houston, 1994). Predation risk often varies between habitats, and divers should respond to this factor as well.

5.2. Assumptions and future directions

An important assumption of this model is that a diver faces risk only while at the surface. In some cases, however, the diver may be at risk while submerged. For example, some marine mammals are at risk from several species of large sharks (e.g., sixgill shark, *Hexanchus griseus*) only while at depth (Ebert, 1994; Heithaus, 2001a). While the presence of such predators likely influences a diver's allocation of time over the dive cycle, such situations are beyond the scope of our model. Nonetheless, the surface will be the most, or only, dangerous location for many divers, particularly those under risk only from aerial predators. In systems where subsurface predators of air-breathing species select prey in the upper portion of the water column, as appears to be the case for tiger and white sharks, divers may also be under greatest risk while at the surface (Le Boeuf and Crocker, 1996; Strong, 1996; Heithaus, 2001b; Simpfendorfer et al., 2001; Heithaus et al., 2002b).

Throughout this model, we consider only how an individual diver should allocate time over the dive cycle or select a foraging habitat in the absence of other individuals. Individuals of some sea bird species dive alone when catching prey to provision offspring, but form groups when diving to self-feed (e.g., rhinoceros auklet, *Cerorhinca monocerata*, Davoren and Burger, 1999). Forming groups likely influence both the risk faced by an individual forager (perhaps through dilution: Kramer and Graham, 1976; see Schenkeveld and Ydenberg (1985) for a pirating risk analogy) and their energy-intake rate (in either a positive or negative fashion), and thus may create further tradeoffs.

Our model assumes that a diver does not use anaerobic respiration. While empirical studies suggest that most dives are within the aerobic dive limit, anaerobic respiration may be adaptive in some foraging situations (e.g., Western Grebes, *Aechmophorus occidentalis*, Ydenberg and Clark, 1989; hooded seals, *Cystophora cristata*, Thompson and Fedak, 2001). While not included in this model, understanding how predation risk influences a diver's use of anaerobic respiration may be a fruitful avenue of study. Anaerobic respiration eventually results in extended surface periods for recovery (Boyd, 1997), and might increase risk to a diver in situations with UIR and IIR. However, the energetic advantages of using such respiration may at times outweigh this cost, particularly when divers forage on ephemeral patches of pelagic prey (Ydenberg and Clark, 1989). Divers facing DIR may be more willing to use anaerobic respiration, as the added energetic benefits would not result in increased risk.

Divers can modify ascent and descent rates (e.g., Gentoo penguins, *Pygoscelis papua*, Wilson et al., 1996), and might also change foraging depths during a foraging bout. Also, depth-specific upthrust forces caused by

buoyancy affect foraging costs, and make descents more costly than ascents (Wilson et al., 1992). We assumed that (a) travel time is directly related to diving depth, (b) travel and foraging costs per unit time are fixed, and (c) only one foraging depth is chosen for a particular foraging bout. Empirical studies suggest that the ascent and descent rate assumption may be valid in some cases; pochards showed a constant ascent and descent rate when foraging depth increased (Carbone and Houston, 1994). The assumption of no buoyancy costs may affect the magnitude of difference between s^* and s_r^*, but is unlikely to qualitatively affect our predictions. Buoyancy considerations will likely be most important if divers responding to risk shift to shallower food patches (see Fig. 1).

We assume that foragers use a pure tactic, whereby they do not vary their surface time throughout a foraging bout and spend an amount of time at the foraging depth that is a function of the preceding surface period. This assumption allows us to make general predictions about how divers might forage while under the risk of predation. Diving, however, is a dynamic process, in which the decision to end a dive may be evaluated at very short-term intervals (e.g., second by second) and be affected by the probability of prey capture, and the diver's energetic state and remaining oxygen reserves at that particular point in the dive (Ydenberg and Clarke, 1989; Beauchamp et al., 1992). For example, divers that are single-prey loaders (e.g., common eiders, *Somateria mollissima*) will return to the surface as soon as a prey item is captured, and optimal prey-searching behavior for patchy prey may cause animals to terminate dives well before the maximum attainable bottom time is reached (Beauchamp et al., 1992). Furthermore, divers may not forage to maximize time underwater for a given surface interval in order to maintain oxygen reserves for predator avoidance in situations where they may be forced to dive if encountering a predator upon surfacing. Dynamic state variable modeling (Clark and Mangel, 2000) would be the appropriate technique for considering how time-structured diving decisions might affect the predicted responses to predation risk.

Finally, this model addresses how foraging divers should respond to predation risk. While some species generally dive only while foraging (e.g. seabirds, some pinnipeds), others spend most of their lives submerged and engage in diving behavior that does not involve foraging (e.g. sea turtles, cetaceans, some pinnipeds) (Boyd, 1997). Although our model is most applicable to foraging divers, the principles apply to divers that are not foraging. Thus, our model can be modified to predict decisions by resting or traveling divers based on the assumption that this might minimize energetic expenditure (rather than energetic intake) divided by predation risk.

Although much progress has been made in the decade and a half following Kramer's (1988) pioneering model of optimal diving, the influence of predation risk on diving decisions remains largely unknown. Our model suggests that predation risk may cause divers to change their optimal allocation of time over the dive cycles that comprise a foraging bout. These deviations may affect habitat use and likely have important fitness consequences. Furthermore, human disturbance (e.g. motorboats) may cause divers to modify their surface intervals and dive cycles (e.g., Janik and Thompson, 1996), and animals often respond similarly to disturbance and predation risk (Frid and Dill, 2002). If divers respond to human disturbance in a manner similar to predators, our model could contribute to understanding and mitigating the impact of human disturbance on some species of aquatic air-breathers. Future testing and refining of these ideas should provide stimulating avenues for ecological and conservation research.

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