

Substrate Partitioning among Non-territorial Damselfishes during Spawning in Northern Taiwan¹

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Rong-Quen Jan and Kun-Hsiung Chang (1993) Substrate partitioning among non-territorial damselfishes during spawning in northern Taiwan. *Bull. Inst. Zool., Academia Sinica* 32(3): 184-193. We assess the significance of substrate utilization and partitioning during spawning to the mechanism underlying the structure of reef-fish assemblage. Underwater observations of damselfish were made in the subtidal waters at Kueihoe, on the northern coast of Taiwan, between the months of April and October in both 1986 and 1990-91. Over 5,000 nests were observed for six non-territorial damselfish species, including *Abudefduf bengalensis*, *Abudefduf coelestinus*, *Abudefduf vaigiensis*, *Chromis fumea*, *Neopomacentrus taeniurus* and *Pomacentrus coelestis*. The data collected from these observations were used in an analysis of the overlapping of resource utilization. Our results show that the distribution of overlap indices was positively skewed, thereby indicating specific damselfish preference in spawning substrate utilization. In other words, the spawning substrate of non-territorial damselfishes in the observed reef environment was finely partitioned. This finding supports that section of the resource partitioning hypothesis concerning the mechanisms which account for the coexistence of these damselfish species.

Key words: Community structure, Nesting substrate, Overlap index, Resource partitioning, Spawning site, Substrate.

Resource partitioning is a central issue regarding the coexistence of fishes in diverse coral reef fish communities (Smith and Tyler 1972, Sale 1978 1980, Gladfelter and Gladfelter 1978, Smith 1978, Den Boer 1986, Mapstone and Fowler 1988). It has recently been suggested that the community structure of coral reef fish is orderly and predictable if spatial and temporal scales are large. That is, it is probable that deterministic selec-

tion coefficients will be produced in a fish population (Clarke 1977 1988, Ogden 1986, Roberts 1986). However, those deterministic factors underlying succession of a community are still unclear. Resource partitioning is a factor worthy of further attention, since specialization in resource utilization is one of the ways by which order is created within a fish community.

Space and food are the resources that have attracted most attention in attempts to

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understand resource partitioning among reef fishes (food, Chave and Eckert 1974, Hobson 1974, Hobson and Chess 1978, Wolf 1985, Neudecker 1985, Roberts 1987; habitat, Robertson and Lassig 1980, Waldner and Robertson 1980, Carpenter *et al.* 1981, Sale *et al.* 1984, Roberts 1986). Of these two, living space is likely to be more important (Fishelson 1980, Sale 1980). In a reef environment, it has been recognized that coral reef fishes partition substrate (their major spatial element) for habitat (Smith and Tyler 1972, Chave and Eckert 1974, Waldner and Robertson 1980, Roberts 1986). There is a considerable amount of information available concerning substrate partitioning, particularly on territorial fishes — those which are closely associated with substrate (Robertson 1984, Ebersole 1985). However, while substrate is considered a resource insofar as it provides habitat (in the sense of physical environment), it is unlikely that substrate is limiting for all coral reef fishes, since there is little evidence that substrate partitioning exists in those fishes categorized as habitat generalists (Fishelson 1980, Sale 1980). If resource partitioning is to be considered the primary mechanism underlying coexistence, we suggest that — in addition to being partitioned as physical habitat — substrate may also be partitioned according to other characteristics or resource dimensions. In this paper, we considered the utilization of substrate during spawning as one aspect of substrate partitioning among habitat generalists.

There are many habitat generalists which spawn demersally (Myrberg *et al.* 1967, Fishelson *et al.* 1974, Mapstone and Wood 1975, Chang and Jan 1983, Thresher 1984), or pelagically over preferred spawning sites (Johannes 1978, Robertson 1983, Warner 1984 1987). These fishes are not otherwise associated with specific types of substrate, but may require an appropriate kind of substrate upon which to deposit their eggs during spawning. Suitable substrate may

then be considered an important resource, and thus a greater demand for such substrate may be expected when these demersal spawners are actively spawning. If a particular substrate is in short supply — as has been assumed in the resource-partitioning hypothesis of reef fish community structure (Ogden 1986, Roberts 1986, Clarke 1988, Mapstone and Fowler 1988) — then we may be able to predict the partitioning of substrate to avoid competition.

To test this hypothesis, we investigated the degree of spawning substrate overlap among demersal spawners — especially those whose spawning periods overlap in time. We considered two aspects of spawning substrate: *spawning site* refers to the location on the reef where spawning occurs, while *nesting substrate* refers to the substrate on which nests are formed. We did this on the presumption that the contributions of these two aspects to the overall fitness of the spawning fish are dissimilar; this is because nesting substrate functions as an arena within which parental investment — egg caring in particular — can be extended to fertilized eggs (Blumer 1979, Perrone and Zaret 1979, Potts 1984 1985). Spawning location presumably have more to do with environmental factors such as current movement and predation on larvae, subsequently affecting the destiny of hatchlings (Johannes 1978, Barlow 1981, MacDonald 1981).

Damselfishes were selected for observation because they meet our theoretical requirements: they are composed of both habitat specialists and habitat generalists, yet all species studied up to now are known to be demersal spawners (Thresher 1984). Since we concentrated on substrate partitioning among habitat generalists, those species which establish long-term territories were excluded from this investigation — principally because they are habitat specialists rather than habitat generalists (Robertson 1984, Ebersole 1985).

MATERIALS AND METHODS

Underwater observations were made in a small bay at Kuei-hoe village, eastward of Yeh-liu Peninsula on the northern coast of Taiwan (121°41'E, 25°12'N), in late April and mid-October of 1986, 1990, and 1991. Except for a fishing harbor near the village, the shoreline consists of giant sandstone rocks. The northern part of the study area is composed of a reef, while the southern part (adjacent to a beach) is generally sandy. The study site was previously described in greater detail in Jan and Rupert (1992a 1992b). Nine damselfish species are commonly found in the study area: *Abudefduf bengalensis*, *A. coelestinus*, *A. vaigiensis*, *Chromis fumea*, *C. notata*, *Neopomacentrus taeniurus*, *Pomacentrus coelestis*, *Stegastes fasciolatus*, and juvenile *Dascyllus trimaculatus*. For the most part, the territorial *Stegastes fasciolatus* is the dominant reef framework species.

For data collection the subtidal area was divided according to the underwater topography into six zones: surge zone, reef

flat, reef channel, reef edge, reef front, and patch reef. Brief descriptions of these zones (Fig. 1) are:

Surge zone: shallow subtidal region adjacent to shore.

Reef flat: common reef framework between surge zone and reef front.

Reef front: outer reef framework where reef slope begins.

Reef channel: a trough penetrating the reef framework; embayment adjacent to sandy area.

Reef edge: edge of reef framework around reef channel.

Patch reef: small reef surrounded by flat, sandy bottom.

During the survey, all spawning sites were recorded; spawning sites are described here in terms of the reef zone where nests were found. Moreover, since damselfishes in our study area build nests on various types of substrate microstructure — including the top of the reef framework, the side face of the reef outcrop, caves which

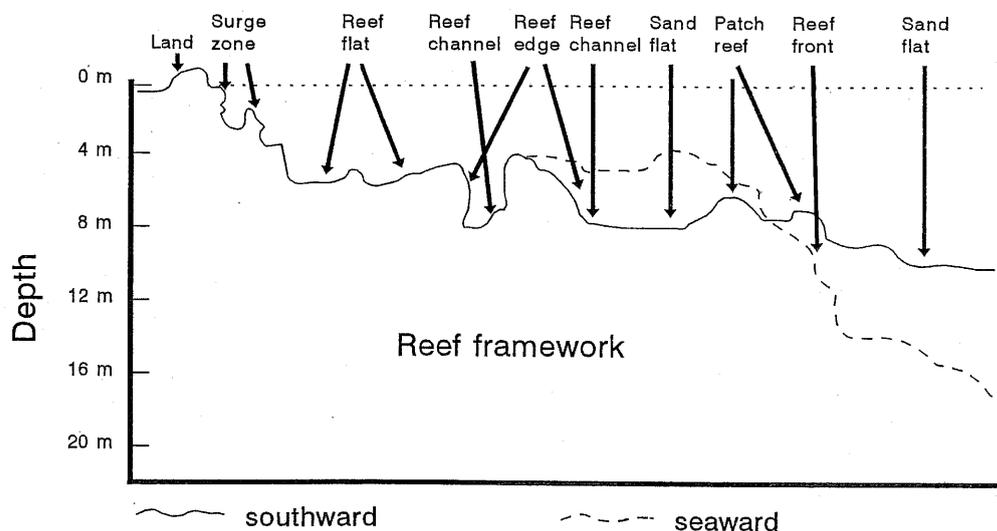


Fig. 1. Profile of the study area showing reef framework. (Widths of zones are not to scale.)

open onto the side face, the underside of reef overhangs, and pockets or burrows on the sea bed (Fig. 2) (Jan and Ormond 1992a) — information on the type of substrate used for each nest was also collected.

Data analysis

Only data collected on non-territorial damselfishes were used in our quantitative analysis. Two sets of frequency data were collected for each species: the first concerned spawning site and was based on the number of nests found in different topographical zones; the second dealt with nesting substrate and was based on the number of nests found on different types of substrate. In order to equally weigh all species, relative frequency rather than observed frequency was used in our analysis. These relative frequencies were obtained by calculating the number of nests in each zone or on each type of substrate per 100 nests for each species.

An overlap index (O_{ij}) between two subject species was calculated for relative frequencies using the following formula (Pianka 1973):

$$O_{ij} = \left(\sum_{a=1}^m P_{ia} P_{ja} \right) / \left(\left(\sum_{a=1}^m P_{ia}^2 \right) \left(\sum_{a=1}^m P_{ja}^2 \right) \right)^{1/2}, \quad (1)$$

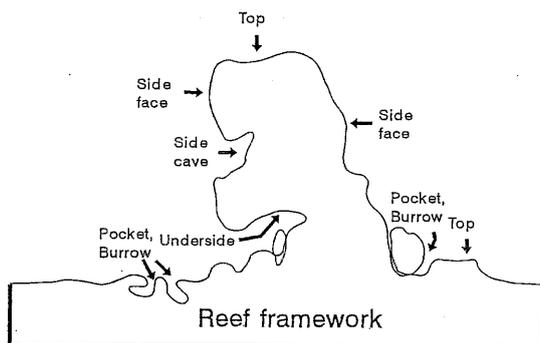


Fig. 2. Types of nesting substrate.

where O_{ij} is the mutual overlap index between i th and j th species. P_{ia} and P_{ja} are the relative frequencies of species i and j , respectively, using the a th resource partition.

Since overlap indices calculated via the above method are symmetrical — that is, $O_{ij} = O_{ji}$ — a test of interdependence of spawning site and nesting substrate can be done using the method described by Slobodchikoff and Schulz (1980):

$$I_{ij} = \left(\left(\sum_{a=1}^m P_{ia}^2 \right)^{1/2} \left(\sum_{a=1}^m P_{ja}^2 \right)^{1/2} + \left(\sum_{b=1}^n P_{ib}^2 \right)^{1/2} \left(\sum_{b=1}^n P_{jb}^2 \right)^{1/2} \right) / \left(\left(\sum_{a=1}^m P_{ia}^2 + \sum_{b=1}^n P_{ib}^2 \right) \left(\sum_{a=1}^m P_{ja}^2 + \sum_{b=1}^n P_{jb}^2 \right) \right)^{1/2}, \quad (2)$$

where I_{ij} is the interdependent index between the two resources calculated from species i and j (a , nesting zone; b , spawning substrate). I_{ij} lies between 0 and 1; if the resources are completely interdependent, then $I_{ij} = 1$, but if the resources are completely independent, $I_{ij} = 0$ (Slobodchikoff and Schulz 1980).

RESULTS

Among the nine common damselfishes previously listed, spawning was observed in seven species (*Chromis notata* and *Dascyllus trimaculatus* excluded). Detailed information on nest formation and nest distribution have been previously described by Jan (1991), and Jan and Ormond (1992a 1992b). A total of 5,169 nests were found for six species, the exception being the territorial *Stegastes fasciolatus* (Table 1). Moreover, because none of these nests were observed on the reef flat, that zone was not included in our data analysis.

Our results show that damselfish species appear to differ from each another by building nests at different zones — as indicated by variation in nest distribution. For example, *Abudefduf vaigiensis* mainly chose to spawn

Table 1. Number of nests found in different zones.

Species names (with abbreviation)		Zones					Total
		Surge zone	Reef edge	Reef channel	Patch reef	Reef front	
<i>A. bengalensis</i>	Ab	16		3			19
<i>A. coelestinus</i>	Ac		8	48		15	71
<i>A. vaigiensis</i>	Av		1,043	102			1,145
<i>C. fumea</i>	Cf			211	2,163		2,374
<i>N. taeniurus</i>	Nt				33		33
<i>P. coelestis</i>	Pc			1,304	223		1,527

Table 2. Number of nests found on different types of substrate.

Species	Substrate type					Total
	Top	Side face	Side cave	Underside	Pocket, Burrow	
<i>A. bengalensis</i>		5	6	8		19
<i>A. coelestinus</i>		12	27	32		71
<i>A. vaigiensis</i>	17	724	216	188		1,145
<i>C. fumea</i>	1,457	896	21			2,374
<i>N. taeniurus</i>			33			33
<i>P. coelestis</i>				3	1,524	1,527

along the reef edge and reef channel, while all *Neopomacentrus taeniurus* spawned on patch reefs. In addition, the damselfishes observed in this study also tended to use different types of substrate for depositing their eggs (Table 2). In particular, *Pomacentrus coelestis* laid its eggs in pockets or burrows while *Chromis fumea* nests were formed mainly on top of substrates.

Overlap indices for the spawning site dimension (equation (1)) are presented in Table 3; these indices range between 0 and 0.99. The frequency histogram for the 15 calculated values is presented in Fig. 3. The distribution of these indices is positively skewed (skewness = 2.98). This distribution indicates that up to 67% of the indices are less than 0.1; however, as both *Chromis fumea* and *Neopomacentrus taeniurus* were

mostly observed spawning on patch reefs, the overlap index between these two damselfishes is notably high (0.994).

Among the six types of substrate, three (side face, underside of overhangs, and lateral cave) were used most often (Table 2). For each pair of damselfish, the overlap index for nesting substrate was calculated; results are presented in Table 3. Figure 4 shows the resultant frequency distribution, which is less skewed (skewness = 1.25) compared to that for spawning site. Nevertheless, with 47% of the indices being less than 0.1, it also indicates a narrow overlapping of resource utilization. It is worth noting that *C. fumea* and *N. taeniurus*, whose spawning sites overlapped notably, strongly differed in their choice of nesting substrate (overlap index = 0.005).

Table 3. Overlap indices for spawning sites and nesting substrates. Species names are abbreviated as in Table 1.

Overlap indices for nesting substrate		Overlap indices for spawning site					
		Ab	Ac	Av	Cf	Nt	Pc
Ab	Ab	1	0.029	0.005	0.009	0	0.083
Ac	Ac	0.987	1	0.121	0.036	0	0.335
Av	Av	0.709	0.596	1	0.006	0	0.053
Cf	Cf	0.101	0.064	0.287	1	0.994	0.258
Nt	Nt	0.351	0.408	0.209	0.005	1	0.153
Pc	Pc	0.002	0.002	0.001	0	0	1

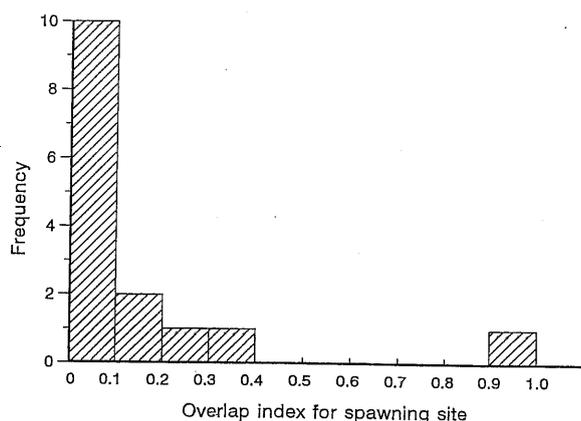


Fig. 3. Frequency histograms of overlap indices for spawning site.

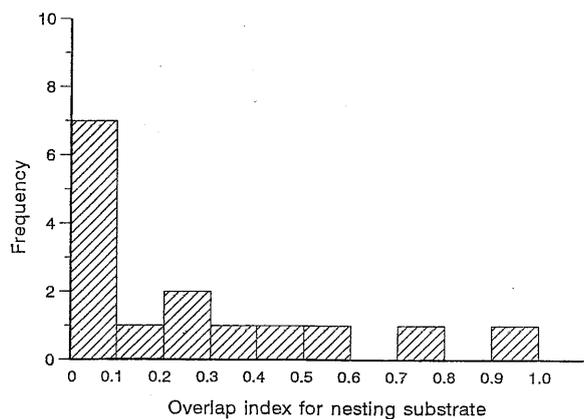


Fig. 4. Frequency histograms of overlap indices for nesting substrate.

Our calculated overlap indices of paired species over the two spawning resource aspects are highly interdependent, as shown by the high values of I_{ij} (0.75-1.0) (Table 4). Consequently, the overall overlap index for each species pair was obtained from the arithmetic averages of the corresponding overlap indices from the two resources (Cody 1974, Pianka 1975, Slobodchikoff and Schulz 1980). These combined overlap indices are presented in Table 5, and their frequency distribution is shown in Fig. 5. The distribution of the combined overlap indices is positively skewed (skewness = 1.02), as

Table 4. Indices of the interdependence of resources in terms of utilization of two resources (spawning site and nesting substrate) by pairs of species. Species names are abbreviated as in Table 1.

	Indices of the interdependence of resource					
	Ab	Ac	Av	Ch	Nt	Pc
Ab	1.00	0.99	0.99	0.76	0.93	0.77
Ac		1.00	0.99	0.75	0.92	0.76
Av			1.00	0.79	0.94	0.80
Ch				1.00	0.95	1.00
Nt					1.00	0.95
Pc						1.00

Table 5. Combined overlap indices on the utilization of substrate during spawning among six damselfish species. Species names are abbreviated as in Table 1.

Combined overlap indices						
	Ab	Ac	Av	Cf	Nt	Pc
Ab	1	0.508	0.357	0.055	0.176	0.042
Ac		1	0.358	0.050	0.204	0.168
Av			1	0.146	0.104	0.027
Cf				1	0.499	0.129
Nt					1	0.077
Pc						1

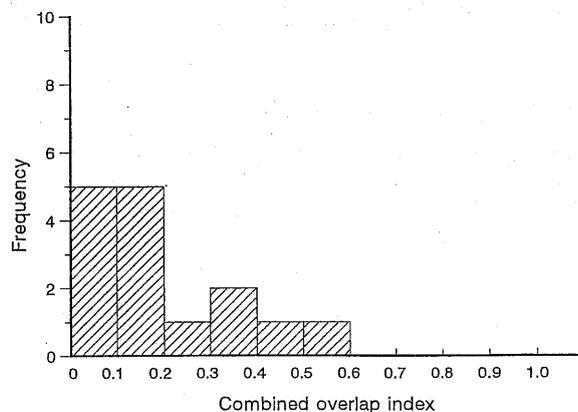


Fig. 5. Frequency histograms of combined overlap indices.

are the overlap indices obtained from the separate analyses of the two resources. Among these damselfish species, 93% of their combined overlap indices were found to be lower than 0.5.

DISCUSSION

In general, midwater-damselfishes do not hold on to permanent territories; neither do damselfishes with large home ranges.

They do, however, need substrates for spawning. Ethological studies have shown that damselfish have a preference for specific nesting substrates, or at the least discriminate between the physical structure of nesting substrates (Swerdloff 1970, Sale 1971, Stanton 1985, Jan and Ormond 1992a). Thus, the question arises as to whether or not these fish can succeed in obtaining their optimal spawning substrate in environments where their preferred substrates are already occupied by other marine organisms, *i.e.*, territorial fishes, coelenterates, sponges, polychaetes, etc. (Palaganas and Alino 1985, Buckley 1985, Jan and Chang 1991). Analyses of the partitioning of substrate utilization do not provide adequate information on interactions between fishes or between different cohorts. However, they do provide information which allows us to better understand the probability of competition between different species.

In this study the substrate resource was divided in two aspects — spawning site and nesting substrate. In practice, spawning sites were categorized in accordance with subtidal topography. The results of our study show that the spawning sites — as well as the nesting substrates — of non-territorial damselfishes are partitioned, as demonstrated by the low combined overlap indices (Tables 4 and 5).

This study's frequency distribution pattern of the combined overlap index (Fig. 5) is similar to that for desert lizards in Australia (Pianka 1975, obtained from similar methods used for food, place, and time resources); however, it departs from that shown for American bird communities (Cody 1974). Absolute values of combined overlapping that are "tolerable" (*i.e.*, do not result in severe competition) are difficult to determine. According to niche theory, if the overlap is very small, or if the resources are super-abundant, then species can coexist in what are essentially separate niches (Giller 1984,

Putman and Wratten 1984). If niches overlap to a great extent, and resource availability in the overlap zone cannot meet demand, then the abundance of less efficient species will be limited by their interactions with more efficient ones (Pianka 1981, Giller 1984, Schoener 1987). Based on this assumption, it is possible to predict the competitive outcome of different degrees of niche overlap between two species.

We propose that spawning site and nesting substrate are additional dimensions of the spatial resources which are partitioned among damselfishes, further supporting the hypothesis that our observed fish assemblages may have been partly structured by the partitioning of these resources. This assumption may also help explain the coexistence of damselfish species in a reef environment. It should be emphasized, however, that the partitioning of spawning substrate is unlikely to have evolved in isolation; the process of spawning substrate partitioning is likely to have been broadly integrated with the partitioning of other resources such as food and habitat. Thus those selective pressures associated with resource utilization by fishes in a reef environment are most likely more complex.

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台灣北部非領域性雀鯛產卵基質的分配

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本項研究的主要目的，在於評估魚種生殖時產卵基質的使用及分配情形在礁岩魚類群聚的形成中所具有的意義。我們以雀鯛科的魚類做為研究的材料，資料的收集在1986、1990、1991年每年的四月到十月這一期間內以潛水的方式進行，地點為台灣北部龜吼村附近的亞潮帶海域。所收集到的非領域性雀鯛的生殖巢資料共5,169筆，這些生殖巢分別屬於六個魚種，亦即孟買雀鯛 *Abudefduf bengalensis*、六帶雀鯛 *A. coelestinus*、條紋雀鯛 *A. vaigiensis*、燕尾光鰓雀鯛 *Chromis fumea*、藍帶雀鯛 *Neopomacentrus taeniurus* 以及變色雀鯛 *Pomacentrus coelestis*。這些築巢資料經做種間資源利用的重疊度分析，結果顯示，重疊指數的分布具有正偏歪的現象，此表示各雀鯛魚種在其築巢基質的選擇上具有偏好，而從另外一個角度來看，亦即於岩礁環境中，非領域性雀鯛在產卵基質的利用上有明顯的分配現象。因此對於這些雀鯛魚種共存現象的維持，本項結果支持依據「資源分配」這一假說所提出來的解釋。

Establishment of an *In Vitro* Bioassay for Measuring Duck Serum Luteinizing Hormone Levels: Rooster Testicular Testosterone Formation System¹

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San-Tai Shen and John Yuh-Lin Yu (1993) Establishment of an *In vitro* bioassay for measuring duck serum luteinizing hormone levels: rooster testicular testosterone formation system. *Bull. Inst. Zool., Academia Sinica* 32(3): 194-203. The purpose of this study was to establish a simplified rooster dispersed testicular cell testosterone formation system for an *in vitro* bioassay of purified luteinizing hormones (LHs) and circulating LH of ducks. Dispersed testicular cells were prepared from 3- to 4-month-old roosters. Five grams of decapsulated testes were dispersed in 50 ml Medium 199, first with a dropper, then with a 25-ml glass syringe, until a homogeneous suspension was obtained. Following preincubation at 37°C for 0.5 hr, dispersed testicular cells (5×10^6 interstitial cells/vial) were incubated with various doses of LHs, pituitary extract, or serum in Medium 199 with 0.125 mM MIX (pH 7.40) at 37°C for 4 hr in a Dubnoff incubator shaking at 100 cycles/min under continuous aeration of 95% O₂ – 5% CO₂. Testosterone levels in the incubated medium were then measured by radioimmunoassay.

Parallel dose-related testosterone formation curves were produced with mammalian LHs, avian LHs, and piscine gonadotropin (GTH); other pituitary hormones (follicle stimulating hormone, thyroid stimulating hormone, growth hormone, and prolactin) were ineffective in inducing testosterone formation. The sensitivity of this system was measured at 0.1 ng/vial and 0.2 ng/vial for purified ovine LH (NIADDK-oLH-25) and duck LH (ASIZ-dLH-1), respectively. Duck sera produced dose-related testosterone formation curves parallel to purified duck LH. Elevated LH levels in the blood circulation of ducks following GnRH injection were successfully measured by the present method. This system for the testosterone formation of rooster dispersed testicular cells was therefore found to be suitable for *in vitro* bioassays of purified mammalian and avian LHs, as well as the LH contents of duck pituitary and blood serum.

Key words: *In vitro* LH bioassay, Rooster testicular testosterone formation, Vertebrate LHs, Duck pituitary and serum LHs.

The steroidogenesis of gonadal cells in many vertebrate species has been studied *in vitro* and used to assess the biological

potency of gonadotropins (GTHs) from homologous or heterologous species. Examples include rats (Dufau *et al.* 1974 1976), mice (Steiner *et al.* 1980, Yu *et al.* 1981),

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